THE UNIVERSITY OF ALBERTA

A REVISION OF THE GENERA *PHILOPHUGA* MOTSCHOULSKY AND *TECNOPHILUS* CHAUDOIR, WITH NOTES ON THE NORTH AMERICAN CALLIDINA (COLEOPTERA: CARABIDAE)

by

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies for acceptance, a thesis entitled "A Revision of the Genera Philophuga Motschoulsky and Tecnophilus Chaudoir, with notes on the North American Callidina (Coleoptera: Carabidae)" submitted by David John Larson in partial fulfilment of the requirements for the degree of Master of Science.

ABSTRACT

A taxonomic revision of the species of the North American genera Philophuga Motschoulsky and Tecnophilus Chaudoir is presented. Four species and four subspecies of Philophuga are recognized. The taxa Philophuga horni Chaudoir and Philophuga amoena LeConte are grouped with P. viridis Dejean to form a polytypic species, and P. viridis klamathea new subspecies is described. Infernophilus new genus, is erected to contain the species castaneus Horn, formerly included in Philophuga. The following names are synonymized for the first time: P. lauta Casey (= P. viridis viridis Dejean), P. canora Casey (= P. viridis amoena LeConte), P. obscura Casey (= P. viridis amoena LeConte), P. cobaltina Casey (= P. viridis horni Chaudoir), P. uteana Casey (= P. viridis horni Chaudoir). The name Tecnophilus pilatei Chaudoir is removed from synonymy to the name of a species. Two subspecies of a second species of Tecnophilus are recognized; T. c. croceicollis Menetries and T. c. peigani new subspecies.

Geographical variation among the populations of Philophuga viridis Dejean and Tecnophilus croceicollis Menetries is analyzed.

The structure of the female stylus is described for the Callidina and is used to erect a classification of the North American species of this group.

Larvae of Philophuga viridicollis and Tecnophilus croceicollis are described.

The method of oviposition and the habitats of the adults are described.

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1. INTRODUCTION

My interest in this group of carabids began with the discovery of specimens of <u>Tecnophilus</u> <u>croceicollis</u> Menetries in southern Alberta. Examination of specimens of <u>T. croceicollis</u> from other localities indicated that considerable geographic variation was exhibited by specimens belonging to this species, and also suggested to me that the genus <u>Tecnophilus</u> contained more than the one recognized species. I decided to include the genus <u>Philophuga</u> in this study because of the similarities in both morphological characteristics and distribution patterns shown by members of the genera <u>Philophuga</u> and <u>Tecnophilus</u>. I undertook a brief study of the subtribe Callidina to elucidate the relationship between these two genera, and to the genus <u>Callida</u>.

The complexity of the tribe Lebiini has led many authors to divide it into subtribes. The concept of the supra-generic grouping, the Callidina, was first introduced by Chaudoir (1872). Chaudoir's Callides was a heterogeneous assemblage of lebiine genera which included some genera not belonging here, and excluded others, such as <u>Philophuga</u>, previously described by Motschoulsky (1859), which are certainly callidines. When Chaudoir (1877) later described <u>Tecnophilus</u>, a callidine genus in even the strictest sense, he placed it in his unspecified grouping Mimodromiides.

Horn's (1882) synopsis of the Tribe Lebiini was the next, and last comprehensive work on the North American Callidina. Although Horn did not recognize any formal subtribal groupings, he did indicate that a close relationship existed between <u>Callida</u>, <u>Philophuga</u> and <u>Plochionus</u>. Without reference to the genitalic structures, Horn described <u>castanea</u>

as a member of Philophuga. He also suggested that a relationship may exist between Tecnophilus Chaudoir and Euproctus Solier (= Euproctinus Leng and Mutchler) and that these two genera are rather separate from Callida.

Since Horn's time, the only work on a large group of North American lebiines has been Madge's (1967) revision of Lebia Latreille.

Casey (1913 and 1924) described six species of Philophuga, five of which are here regarded as conspecific with previously described species.

Jeannel (1942 and 1949) treated the lebiine faunas of France and Madagascar respectively. He recognized the formal grouping Callidinae but did not present any truly diagnostic characters to define it.

Recently, two major works by Jedlička (1963) and Habu (1967) have appeared, dealing with the Asian Lebiini. Habu presents the best sub-tribal classification yet proposed, based largely on the structure of the legs, mandibles and female ovipositor. Habu's definition of the Callidina is followed in part in this study.

2. MATERIALS, METHODS AND TAXONOMIC CHARACTERS

2.1. Materials

I have examined over 1200 specimens of adults and larvae of the genera Philophuga and Tecnophilus in the course of this study. Most of these specimens were obtained on loan from various museums in Canada and the United States. Many specimens of Tecnophilus were collected by myself on a number of field trips to southeastern Alberta, and on an extended trip through southwestern United States. Larvae were reared in the laboratory from eggs laid by captive adults.

Following the description and discussion for each species and subspecies, a list of the localities from which specimens have been examined is presented. The localities are listed alphabetically, in the following order; country, province or state, county and specific locality. Following this, the collector's name and the museum in which the specimen is stored are listed in parentheses.

Abbreviations for museums from which specimens were seen, are as follows:- AMNH - American Museum of Natural History; Car.M. - Carnegie Museum; CAS - California Academy of Sciences; CNC - Canadian National Collection, Ottawa; CNHM - Chicago Natural History Museum; CU - Cornell University; DAL - Canada Department of Agriculture Research Station, Lethbridge, Alberta; INHS - Illinois Natural History Survey; IUM - University of Idaho; KUM - University of Kansas; OUM - Oregon State University; MUB - University of Montana, Bozeman; MCZ - Museum of Comparative Zoology; SJSC - San Jose State College, California; UASM - University of Alberta, Strickland Museum; USNM - United States National Museum; and WUM - University of Washington, Seattle.

2.2 Methods

2.2.1 General

Observation and comparison were the methods used (Ball, 1966). Observations were made of both morphological and biological features of both preserved and living specimens of the subtribe Callidina. Using these observations, comparisons were made between different population samples in order to ascertain similarities and differences. Most observed characteristics were compared independently and were weighed subjectively depending upon the circumstances. That is, in one situation a given character may have been regarded as possessing no discriminatory value, while in another situation it may have been judged important. However, in dealing with variation in one species, Tecnophilus croceicollis, several characters were compared simultaneously and the weights for each of these characters were calculated according to their individual statistical discriminatory value, regardless of other considerations.

2.2.2. Criteria for Species, Subspecies and Genera

The multi-dimensional definition of the species (Mayr, 1963) has been used as the underlying basis for the taxonomy in this study. The taxa assigned to the species category are less arbitrary than taxa assigned to lower or higher categories, hence the species category forms the basis around which a classification is built. Because it is difficult to make the necessary tests on a population to prove the principal criterion for recognizing a species, that is, genetical isolation from other such groups, this information must be obtained indirectly.

In this study, evidence interpreted as indicating specific identity, is provided by: forms which overlap geographically but do not intergrade in their diagnostic characters in the area of overlap; and allopatric

forms in which geographically intermediate specimens do not show intermediate states in their diagnostic characters. For example, the two species Tecnophilus croceicollis Menetries and T. pilatei Chaudoir are primarily allopatric, and their members can be consistantly distinguished from one another on the basis of several characters. However, in the vicinity of Brownsville, Texas, the ranges of these two species overlap, yet the diagnostic characters still hold and permit complete segregation of members of each of these species. I assume that maintenance of these differences is the result of reproductive isolation between these two groups.

I have recognized subspecies only in cases of concordant non-clinal variation in two or more characters. I have not recognized populations along, or at the end of clines as being subspecifically distinct. Rather an attempt has been made to point out such clines and to describe them when they have been recognized (Mayr, Linsley, and Usinger, 1953). In one species, Tecnophilus croceicollis Menetries, clinal variation occurs in many characteristics, however, two subspecies of this species have been recognized. The new subspecies, T. c. peigani, was recognized because a number of characters, many of which varied clinally, showed a sharp change through a relatively short distance to produce two forms which were remarkably different in general appearance, and could be readily distinguished from one another.

A genus has been defined as "a systematic category including one species or a group of species of presumably common phylogenetic origin, which is separated from other similar units by a decided gap" (Mayr, Linsley, and Usinger, 1953). However, the gap necessary to distinguish between groups of species belonging to different genera cannot be

objectively defined. Rather, this must be decided by the taxonomist on the basis of his knowledge and experience in the group. Consistancy in deciding the nature and size of the gap (degree of morphological difference) required to separate related genera is imperative in producing a uniform and workable classification.

In this study, I have recognized the previously described genera, *Callida*, *Philophuga* and *Tecnophilus*, and have used the degree of morphological difference between these three genera as a guideline by which to recognize other genera within this subtribe. The species *Philophuga castaneus* Horn differs from the other species included in the genus *Philophuga* by at least as much as these species differed from the species included in the genera *Callida* and *Tecnophilus*. For this reason, I removed *castaneus* from *Philophuga* and proposed the new genus *Infernophilus* to contain it. Recognition of *Infernophilus* is consistant with the maintenance of *Callida*, *Philophuga* and *Tecnophilus* as distinct genera.

2.2.3. Morphological Methods

To examine characters of the wings and of the genitalia, the specimens were first relaxed by placing them in boiling water for five to ten minutes. After this time, the specimens were sufficiently pliant to allow the elytra to be lifted so that the hind wings could be examined. This was adequate to determine the relative size of the wings. However, in cases where it was necessary to study the pigmentation of the wings, the hind wing was removed by breaking it off near the base. The wing was unfolded and first studied in water, then flattened out and glued to a card which was pinned beneath the specimen.

Male and female genitalia were removed from the relaxed specimens by breaking the supporting membranes around the genitalia with a hooked insect pin. The genitalia were removed with a pair of fine forceps. After dissection, the genitalia were placed in cold 10% KOH and allowed to stand overnight to clear the sclerites. The male genitalia were then examined with a binocular microscope. It was necessary to mount the female genitalia on slides and examine them with a compound microscope at higher magnification.

2.2.4. Preservation of Larvae

To prevent distortion and discoloration of specimens, larvae were killed by dropping them directly into gently boiling water. They were quickly removed and preserved in 70% ethanol. This method of killing extends the larvae to their maximum length and preserves color and hence facilitates later study.

2.2.5. Rearing Methods

Adult specimens of Tecnophilus were reared in the laboratory to obtain eggs and larvae. After collection, five or six specimens were placed in each jar, where mating readily occurred. After mating, the females were removed and isolated in small jars which contained soil a half inch deep and several twigs that permitted the insects to climb. Pieces of mealworm were added for food, and water was sprinkled into the jar weekly.

If adequate food and moisture were provided, the females began to oviposit within a week after mating. The eggs were removed as they appeared, and were placed on a moistened blotter in a petri dish where they were left until hatching occurred. Newly emerged larvae were isolated in

small vials and were fed pieces of various soft-bodied insect larvae. High humidity was maintained by placing a piece of moistened blotting paper in the neck of the vial. Mortality was high, but a number of larvae were reared to the second and third instars.

2.2.6. Measurements and Ratios

Measurements were made of representative specimens of all species and subspecies dealt with in this study. Although they did not provide diagnostic characters for any species, measurements and the ratios derived from them were valuable in the analysis of intra-specific variation. A micrometer eyepiece in a Wild M5 stereoscopic microscope at a magnification of X 50 was used for these measurements.

The total length (TL) of adult specimens was obtained by the addition of three measurements: the length of the head from the anterior margin of the clypeus to the mid-point of the occipital groove (LH); the length of the pronotum along the mid-line (LP); and the length of the left elytron from the apex of the scutellum to the apex of the elytron (LE). Total length (LH + LP + LE) obtained in this way was not affected by contraction or curvature of the specimen. Other measurements taken of adult specimens and their abbreviations are:

Width of pronotum (WP) - width across widest point of pronotum.

Maximum width of head (WH_1) - width of head across eyes.

Width of head between eyes (WH_2) - minimum width of frons between eyes.

Measurements taken of larval specimens are:

Width of head (WH) - width across widest part of head capsule.

Width of pronotum (WP) - width across widest part of pronotum.

Total length (TL) - one measurement of length from the anterior margin of the nasale to the posterior margin of abdominal segment 10.

All ratios used in the text are derived from the above measurements, and are expressed in terms of the above abbreviations.

2.2.7. Analysis of Variation

Specimens from populations that differ slightly and possibly discordantly in a number of characters, may be assigned to the correct population by means of the discriminant function. In the study of such groups, the traditional methods of taxonomy, observation and comparison, do not work well for the mind is incapable of making the numerous summated judgments required.

The discriminant function used in this study has been developed by Dr. J. Stanley (McGill University) (unpublished MS). The method has been used or discussed by Goulden (1952) and Bigelow and Reimer (1954).

Interpretation of the discriminant function is similar to that used for the hybrid index (Freitag, 1965). Using this method, a specimen which deviates from the other members of its population in only one or a small percentage of its total characters, is still assigned to its correct population because of its greater overall similarity to members of that population. This reduces the possibility of mis-identification due to the over-weighing of one character.

2.2.8. Illustrations

Illustrations are presented to augment descriptions. These were prepared with the aid of an ocular grid in a stereoscopic microscope.

The male genitalia have been illustrated for many species even though they usually present few useful characters. Stippling has been used to indicate the folding pattern of the endophallus but as this folding pattern varies with small changes in inversion, it should not be considered as being important in identification.

The slender sub-apical spines on the stylus of the female ovipositor have been included in illustrations of the styli. Both dorsal and ventral spines have been shown as though they occurred in the same plane, as this is the way they appear when the stylus is cleared in potassium hydroxide and mounted on a microscope slide.

Distribution maps are presented for all species and subspecies. Also maps summarizing data on intra-specific variation in the species Philophuga viridis and Tecnophilus croceicollis are included.

2.3 Taxonomic Characters

2.3.1. Taxonomic Characters of Adults

Color.- Within the Callidina, color is useful in the identification and classification of species, and to a limited extent, genera. Non-metallic colors are described by the terms yellow, testaceous (brownish-yellow), rufous (reddish), brown, piceous and black. The color black often has a metallic sheen associated with it. Metallic colors are usually blue or green. To describe variation in certain species, intermediate colors are designated in terms such as blue-green (green predominant) or greenish-blue.

External Morphology.- Punctation and vestiture of the body, while extremely useful for the recognition of species and subspecies with Philophuga and Tecnophilus, are difficult characters to interpret and

quantify. As the setae composing the dorsal vestiture of the body are situated in usually distinct punctures, the punctation of the body often gives an indication of the vestiture. However, in specimens from certain populations, the body is deeply punctate, but the punctures do not bear setae, or bear very inconspicuous setae. Care must be taken to avoid confusing these specimens with normally setose specimens that have been rubbed. The depth and density of the punctures in the elytral striae and on the elytral intervals are important for identification.

To describe the depth of punctation of the body and the depth of the impression of the elytral striae, the terms lightly, moderately and coarsely have been used. These terms are strictly comparative, and have been avoided as much as possible in keys. However, they have been used in descriptions in a comparative sense. Similarily, the terms sparse, moderate and dense have been used to describe vestiture.

The shape of the head shows both intra- and inter-specific variation. Differences in the convexity of the eyes and the constriction of the neck present characteristic forms for certain species. For all species, values for the ratio of the width of the head across the eyes to the minimum width of the head between the eyes has been presented in an attempt to quantify differences in eye convexity. This ratio is not diagnostic of any species but it provides an index of the head shape.

The post-ocular pinch is an impression just behind the posterior dorsal margin of the eye. This pinch is evident but small in most of the Callidina. However, in some of the neotropical species of Callida and in some species of Cymindis this pinch is very strongly developed.

The mouthparts were not found to provide any characters useful for species recognition. They are of value at the generic level, but even here their importance has been overestimated in past works.

The shape of the pronotum is of appreciable diagnostic value. In Philophuga, differences in pronotal shapes between related species are often slight and may be within the range of normal intra-specific variation. In Tecnophilus the shape of the pronotum is much more characteristic of a species, and is usually rather constant within a population sample. The pronotum has been illustrated for most species and subspecies.

The wings present several characters which are considered very important in Philophuga. Wing reduction occurs in this genus and has been used to distinguish between several subspecies of viridis. Also, the degree to which the membranous areas of the wings are pigmented is useful in the recognition of certain species. The wing venation was not found to offer any characters of diagnostic value at either the specific or generic levels.

Habu (1967) made extensive use of the structure of the legs in his classification of the Japanese Lebiini. In the present study, only two characteristics of the legs have been used: the structure of tarsal article 4; and the structure of the tarsal claws. Two forms of tarsal article 4 are found among the Nearctic Callidina, the bilobed form and the emarginate form. These are illustrated in Figures 28 and 29 respectively. The tarsal claws of members of the genus Tecnophilus are simple, while members of the other North American callidine genera possess pectinate claws.

Characteristic arrangements of setae on the ventral surface of the abdomen provide useful characters for the recognition of two genera.

The usual arrangement of setae is: visible sterna 2 to 5 each with a pair of medial setae, sternum 6 with one to three pairs of anal setae. However, members of the genus Plochionus bear, in addition to the above-mentioned setae, a distinctive arrangement of setae on the lateral margins of sterna 4, 5 and 6 (Fig. 26). Members of the genus Infernophilus lack the lateral setae, but sternum 6 possesses a pair of dense brushes of setae (these brushes are much denser in the male than in the female) (Fig. 27).

Male Genitalia.- The structure of the male genitalia is rather consistent within the species of Philophuga and Tecnophilus. The aedeagus (intromittent organ, see Torre-Bueno, 1962) is slightly arcuate, with a prominent rounded apex. The basal piece, the portion of the aedeagus surrounding the basal orifice, varies slightly, but is of minor taxonomic importance. The endophallus is usually unarmed and possesses only poorly defined spiculate fields. However, the genitalia of Infernophilus shows a number of peculiarities (section 5.3).

Female Ovipositor.- The structure of the apical article of the stylus is of great importance in determining subtribal affinities. Basically, the stylus is rectangular in shape, lightly sclerotized and with a setose apical margin. In Tecnophilus pilatei Chaudoir (Fig. 55), and Callida decora Fabricius (Fig. 50), the outer apical corner of the stylus is greatly produced In Infernophilus (Fig. 57) the apex of the stylus is broadly rounded and in Plochionus (Figs. 45, 46) the apex is sharply pointed with a tassel-like arrangement of setae. Small slender spines are scattered over the surface of the stylus but were found to be of little taxonomic value.

2.3.2. Taxonomic Characters of Larvae

As larvae representing only a few of the species of the Callidina have been seen, the variation and distribution of the taxonomically important characters within the subtribe are unknown.

Color.- Color is of considerable value in recognizing the larvae of certain genera. The terminology used to describe color is presented under taxonomic characters of adults.

External Morphology.- Most of the characters and terminology used are taken from Van Emden (1942).

The subtribal character of the presence of a soft membranous pulvillus between the tarsal claws, is difficult to observe in some specimens, hence this structure must be sought for with care.

The dorsal surface of the maxilla of Plochionus possesses short dense setae (Fig. 8). This surface is glabrous or covered with very short stout sensilla in the larvae of the other callidine genera.

The shapes of the pronota of Philophuga (Fig. 9) and Tecnophilus (Fig. 10) have been used to separate the larvae of these two genera. The number of articles in the cerci of 2nd and 3rd instar larvae also separates these two genera, but because this character could not be used to separate the larvae of all instars, it was not used in the key to genera (section 4.3.).

3. TAXONOMY - The Subtribe Callidina

This subtribe may be defined as follows:-

Adult.- Lebiini with the following characteristics: labrum transverse, with six setae along anterior margin; mandible widened toward base, usually with scrobe; labial palpus with penultimate article bisetose, apical article securiform or at least tumid (less in female than in male) and truncate apically; ligula bi- or plurisetose apically, paraglossae not or but slightly extending beyond ligula; mentum usually with a tooth; fore tarsus of male with various number of articles bearing ventral adhesive scales, such scales frequently present on some articles of middle tarsus; tarsal article 4 bilobed, emarginate or simple; prothorax not lobed behind; male genitalia with smaller paramere bilobed apically; female stylus with setose apex.

Larvae.- Head approximately quadrate; epicranial suture wanting, lateral sutures meeting medially at cervical margin; adnasale prominent, covering base of mandibles; nasale broad and prominent, entire or variously emarginate apically; antenna shorter than mandible, article 3 about twice length of article 1, and bearing a short sensory papilla distally; mandible bisetose externally, with reduced or obsolete retinaculum, penicillus present; maxilla without an inner lobe, palpiger evident; labium with a pair of promient apical setae; leg with two equal claws, claws simple or toothed basally; pulvillus present, conspicuous or not; tergites strongly margined anteriorly; abdominal segment 10 with a pair of protrusible vesicles, each bearing a semicircular row of crochets; cerci of four or five articles.

This definition of the Callidina is based upon the limited lebiine fauna of the United States. In this region, the genera <u>Callida</u> Latreille

and Dejean, *Cylindronotum* Putzeys, *Lecalida* Casey, *Onota* Chaudoir, *Philophuga* Motschoulsky, *Plochionus* Wiedemann, *Tecnophilus* Chaudoir, and *Infernophilus* new genus may be assigned to the Callidina.

As defined here, this subtribe is more restricted than conceived by either Chaudoir (1872) or Habu (1967). Habu regarded the shape of the mandibles, the form of the tarsi and the structure of the female ovipositor as the principal subtribal characters. The structure of the tarsus will not unite the Nearctic genera of the Callidina. *Callida* possesses dilated tarsi (Fig. 28) which Habu regards as characteristic of this subtribe. However, the closely related genus *Philophuga*, has only the stout form of tarsus (Fig. 29) and members of the genus *Tecnophilus* possess almost slender tarsi. Both stout and dilated tarsi are found in the genus *Plochionus*.

Habu recognizes three forms of female ovipositor among the Japanese Callidina. These are as follows:-

a) hemisternites transverse, apical segment of stylus long and pubescent apically (Figs. 44-57).

b) hemisternites transverse, apical segment of stylus without terminal setae.

c) hemisternites not transverse, apical segment of stylus without pubescence but with slender spines near apical angle (Fig. 43).

In the Nearctic fauna, no genus occurs which possesses type "b" ovipositor, so I have not been able to determine the relationship between this form of ovipositor and type "a" ovipositor. *Euproctinus* Leng and Mutchler possesses type "c" ovipositor (Fig. 43). As this genus differs from the North American callidines on the basis of the female ovipositor and larval characteristics, I exclude it from the Callidina. Because *Euproctinus*

cannot be assigned to any of the presently recognized subtribes, a new subtribe may have to be proposed to receive it.

The unique brush-like stylus forms an excellent subtribal character for the Callidina, for while the structure shows considerable variation among the genera, the basic form remains recognizable. No other character examined has shown as great a diagnostic value within this group at the subtribal level.

4. LARVAE

The larvae of few species of the tribe Lebiini have been described. This may be the result of at least two factors which make it difficult to obtain the requisite specimens: adults of many species are rarely collected; and the species of at least one genus, Lebia Latreille, have a complex developmental cycle (Lindroth, 1954; Madge, 1967).

4.1. Key to the larvae of the North American subtribes of Lebiini (modified from van Emden, 1942)

1. Retinaculum of mandible vestigial or absent; or if well developed, the cervical groove and keel are present; antenna with article 1 longer than article 3 2

1'. Retinaculum well developed, projecting by more than a third of width of mandible just apicad of retinaculum; head without cervical groove or keel; antenna with article 1 shorter than article 3; tarsal claws toothed or simple . . . . Dromiina

2(1). Tarsus without a pulvillus; tarsal claws with or without a basal tooth, but if tooth present, head with a cervical groove 3

2'. Tarsus with a soft unpaired but more or less bilobed pulvillus between claws; retinaculum vestigial or absent; head without cervical groove; epicranial suture very short or almost absent . . 5

3(2). Retinaculum distinct; cervical groove and keel present except if antennal article 1 is longer than article 3; maxillary stipes rather slender, almost or fully three times as long as width . . . . Coptoderina

3'. Retinaculum small, vestigial or absent; cervical groove absent; antennal article 1 shorter than 3; maxillary stipes robust, at most twice as long as wide 4

4(3). Ligula and its two setae well developed; epicranial suture present though short in some species; cercus of 5-7 articles (but of four articles in at least some first instar specimens) . . . Cymindina

4'. Ligula and its two setae minute or absent; epicranial suture absent; cercus with at most four articles . . . . Lebiina

5(2). Anterior margin of abdominal tergites with margined border . . . . Callidina

5'. Anterior margin of abdominal tergites without margined border . . . . Euproctinus Leng and Mutchler

The Callidina, Cymindina and Lebiina show a number of common features that distinguish these groups from the Dromiina and Coptoderina. However, I do not intend to propose a classification based on characteristics of lebiine larvae. Rather, the known larvae were examined to determine if their characteristics substantiated the generic separations proposed in the Callidina on the basis of characters of adults. Where larvae were available, their characters did support the adult classification.

4.2 Key to the known larvae of the Nearctic genera of the subtribe Callidina

1. Anal vesicles of abdominal segment 10 bearing crochets 2

1'. Anal vesicles of abdominal segment 10 without crochets . . . . Onota Chaudoir

2(1). Maxilla with dorsal pubescence in addition to the usual fixed setae (Fig. 8); nasale narrow, without a deep medial incision (Fig. 7) . . . . Plochionus Weid. p. 20

2'. Maxilla glabrous except for usual fixed setae and short stout sensillae; nasale broad, with a deep medial emargination (Figs. 11-14) 3

3(2). Pronotum quadrate (Fig. 9) . . . . <u>Philophuga</u> Mots. p. 21

3'. Pronotum conical, widest basally and narrowing anteriorly (Fig. 10) . . . . <u>Tecnophilus</u> Chaud. p. 23

4.3.1. <u>Plochionus</u> Wiedemann, 1823

Larvae of only <u>P</u>. <u>timidus</u> Haldeman, 1843 have been seen. The following description is based on five specimens from Kirkwood, Missouri (29/VI/1892, USNM).

Description.- Values for ratios and measurements are: TL, 2nd instar 5.9-7.4 mm; 3rd instar 8.9-10.4 mm; WH/LH, 2nd instar 1.30-1.36 3rd instar 1.24-1.28; WP/WH, 2nd instar 1.20-1.24, 3rd instar 1.25.

Color whitish, head and anterior portion of pronotum yellow; nota two and three, legs, and abdominal tergites testaceous, without metallic lustre; sternites and pleurites testaceous-yellow.

Head broad, more or less quadrate, but somewhat rounded laterally; nasale convex with a prominent relatively narrow tri- or quadridentate medial tooth (Fig. 7); medial suture present but very short, divided into paired sinuate lateral sutures a short distance anterior to cervical margin, cervical border narrow.

Antenna shorter than mandible, with four articles; article 1 broad, about one half length of article 3; article 4 narrow, broadly rounded apically; article 3 with a minute subapical sensillum; subapical setae on articles 3 and 4 only.

Mandible relatively short, slightly and unevenly arcuate, with two external setae; retinaculum minute, rounded and blunt apically; internal apical half of mandible expanded and plate-like; penicillus present at base.

Maxilla (Fig. 8) hairy above, with internal dorsal row of short stiff setae; ventral surface glabrous except for usual long setae; internal lobe absent; palpiger well developed, terminal article of palpus conical and pointed apically; median lobe with two articles, distal article very small.

Labium with medial pair of setae subapical and dorsal, ventral pair of setae also present; palpi of two articles, glabrous, apical article elongate, conical.

Prothorax transversely rectangular, broader and longer than head; lateral margin narrow and faint.

Legs with tarsal claws toothed at base and equal; pulvilli present but inconspicuous.

Anterior margins of tergites and nota strongly margined; tergites entire; ventral sclerites consisting of a ventrite and three pairs of lateral postventrites, all lightly sclerotized and poorly delimited.

Abdominal segment 10 with a pair of protrusible anal tubes, each bearing a semicircular row of crochets; cerci elongate, slender, with five articles in 2nd and 3rd instar larvae (1st instar larvae not seen).

Discussion.- The larva of Plochionus stands apart from the known larvae of the other North American callidine genera on the basis of its setose maxillae, and toothed tarsal claws. Consequently, the position of this genus among the North American Callidina is unclear, and probably cannot be settled until the Neotropical genera are better known.

4.3.2. Philophuga Motschoulsky, 1859

In this genus, the larvae of P. viridicollis LeConte and P. viridis amoena LeConte are known. As only first instar larvae of viridis, and second and third instar larvae of viridicollis were available, I was not

able to find characters that would distinguish between the two species with any degree of certainty. Because of this, a key is not provided, and only the larva of viridicollis is described below.

Philophuga viridicollis LeConte, 1848

A third instar larva, two pupae, an associated adult and a number of exuviae of viridicollis were seen (Rocky Ford, Colorado, Aug. 17, 1915, Hamilton Coll., USNM). Van Emden (1942) included this material under Callida, as C. purpurea Say.

Description.- Values for ratios and measurements of 12 larvae and exuviae are: TL, 3rd instar 9.1 mm; WH/LH, 2nd instar 1.18-1.22 ($\bar{X}$ = 1.20), 2nd instar 1.15-1.20 ($\bar{X}$ = 1.18); WP/WH, 3rd instar 1.18.

Color whitish; head testaceous; body sclerites brown to piceous with a metallic green or violaceous sheen.

Head (Fig. 11) broad, almost quadrate with hind angles broadly rounded; frontal piece broad; sinuate lateral sutures meeting medially at cervical margin, median suture absent; nasale very broad, deeply incised medially, lateral portions tridentate; cervical margin narrow; ocelli six, strongly pigmented.

Antenna slightly shorter than mandible, of four articles; article 4 narrow, subequal in length to article 3, article 1 short; article 3 with a small subapical sensillum; subapical setae on articles 3 and 4 only.

Mandible slender and arcuate, with two lateral setae; retinaculum small and inconspicuous; basal penicillus present.

Maxilla with an internal dorsal row of stout setae plus usual long fixed setae, otherwise glabrous above; inner lobe absent; palpi with well developed palpiger, terminal article narrow and pointed.

Labium broad, bisetose apically, also with a pair of subapical ventral setae; palpi of two articles, glabrous.

Prothorax transversely rectangular (Fig. 9), wider than head; lateral margin strong and complete.

Legs with equal simple claws; pulvilli present.

Tergites entire, with strong anterior borders; lateral margins of meso- and metanota angular; ventral sclerites consisting of a ventrite and three pairs of lateral postventrites.

Cerci with five articles in second and third instars, only subapical setae present; abdominal segment 10 with a pair of eversible anal tubes, each bearing a semicircular row of crochets.

Discussion.- Van Emden (1942), who saw some larval specimens of Callida, keyed Callida and Philophuga to the same couplet, stressing their similarities especially in the shape of the nasale, number of articles in the cerci, and the shape of the tarsal claws. Larval characteristics apparently confirm the close relationship suggested for these two genera by adult characteristics.

4.3.3. Tecnophilus Chaudoir, 1877

The larvae of both subspecies of Tecnophilus croceicollis Men. are known. They were obtained by rearing from adults collected at the following localities: junction of the Lost and Milk Rivers, Alberta (T. c. peigani n. spp.); Cuddeback Lake and Alviso, California (T. c. croceicollis Men.). See section 2.2.5. for rearing methods, and section 6.1 for notes on collecting.

Description.- Values for ratios and measurements are presented in Table 1. The first instar larva of T. croceicollis Men. is illustrated in Fig. 6.

Table 1. Variation in dimensions and ratios among the larvae of

<u>Tecnophilus</u> <u>croceicollis</u> Menetries

Locality	Number of specimens	Instar	Width/length of head		Width pronotum/width head		Width head mm	
			Range	Mean	Range	Mean	Range	Mean
Newark, California	15	1	0.93-1.04	(0.97)	1.07-1.20	(1.14)	0.52-0.54	(0.52)
	6	2	0.97-1.03	(0.98)	1.14-1.31	(1.22)	0.62-0.70	(0.68)
	1	3	1.00		1.17		0.96	
Cuddeback Lake, California	6	1	0.93-1.04	(0.98)	1.16-1.20	(1.17)	0.48-0.50	(0.50)
	2	3	0.94-0.98	(o.96)	1.16-1.18	(1.17)	0.90-0.96	(0.94
Jct. Lost and Milk Rivers, Alta.	13	1	0.96-1.04	(0.97)	1.13-1.29	(1.19)	0.48-0.54	(0.51)
	2	2	0.91-0.93	(0.92)	1.24-1.38	(1.31)	0.78-0.84	(0.81)
	1	3	0.96		1.25		0.88	

Color whitish; head capsule and in many specimens prosternum and anterior half of pronotum yellow; remaining sclerites and appendages piceous, with at least a faint metallic green cast.

Head rectangular (Figs. 12-14); frontal piece broad, medial suture wanting, sinuate lateral sutures meeting medially just anterior to cervical margin; nasale broad, deeply cleft medially, lateral pieces shallowly bifid; posterior constiction of head varied; cervical margin narrow; ocelli six, strongly pigmented.

Antenna shorter than mandible, with four articles; article 1 short, broad, about one half length of article 3; article 4 narrow, widening apically where broadly rounded; subapical setae on articles 3 and 4 only; small sensillum on article 3.

Mandible slender, with two lateral setae; retinaculum small, but evident; basal penicillus present.

Maxilla with internal dorsal row of short, stiff setae and scattered long external setae, otherwise glabrous; palpiger distinct; palpus with three articles, article 3 short, narrow; inner lobe absent; outer lobe with two articles, article 2 very short and narrow, basal article with a single preapical seta.

Labium bisetose apically, also with a pair of ventral setae; palpi with two articles, terminal article short and narrow, pointed apically.

Prothorax somewhat conical (Fig. 10), widest basally and narrowing anteriorly to about width of base of head; variously margined laterally.

Legs with equal simple claws; pulvilli present but reduced.

Tergites and nota margined anteriorly; ventral sclerites consisting of a ventrite and three pairs of postventrites.

Cerci of four articles in all instars; abdominal segment 10 with a pair of eversible vesicles, each bearing a semicircular row of crochets.

Discussion.- I was unable to find characters to distinguish between the larvae of *T. c. croceicollis* and *T. c. peigani*. Table 1 summarizes variation in measured characteristics and ratios among larvae from three localities.

The larvae of *Tecnophilus* are similar to those of *Philophuga*, but they can be distinguished from one another by the character presented in the key. Also, larvae of all instars of *Tecnophilus* have cerci of only four articles. In *Philophuga*, on the other hand, the first instar larvae have cerci of four articles while later instars have cerci of five articles. These differences do not contradict the separation of *Tecnophilus* and *Philophuga* at the generic level.

5. ADULTS

Characteristics common to all members of the subtribe Callidina are presented in section 3. Below is a key to the adults of the North American genera of the subtribe Callidina. Following the key, the genera Philophuga, Infernophilus and Tecnophilus are discussed in detail. I have not had the opportunity to examine the other genera in detail, as the majority of their members are neotropical. Hence, any remarks about the latter group are tentative.

5.1. Key to the adults of the North American genera of the subtribe Callidina (modified from Ball, 1963).

1. Mandible broadly expanded, without scrobe . . . . Onota Chaudoir

1'. Mandible with scrobe 2

2(1). Mentum without a tooth; width of pronotum less than maximum width of head . . . . Cylindronotum Putzeys

2'. Mentum with a tooth; width of pronotum greater than width of head 3

3(2). Lateral margin of abdominal sternum 4 with one seta, sternum 5 with two setae, and sternum 6 with one seta (Fig. 26); hind femur broad . . . . Plochionus Wiedemann

3'. Lateral margin of abdominal sterna 4, 5 and 6 without such arrangement of long setae; hind femur slender 4

4(3). Tarsus with fourth article bilobed (Fig. 28) 5

4'. Tarsus with fourth article at most emarginate (Fig. 29) 6

5(4). Elytra metallic green or blue; pronotum elongate and slender, lateral grooves narrow . . . . Callida Latreille and Dejean

5'. Entire body rufo-piceous, without metallic color; pronotum with lateral grooves broad . . . . *Lecalida* Casey

6(4). Tarsal claws pectinate 7

6'. Tarsal claws simple . . . . *Tecnophilus* Chaudoir, p. 59

7(6). Color dark with metallic blue or green sheen; abdominal sternum 6 with at most four pairs of anal setae . . . . *Philophuga* Motschoulsky, p. 28

7'. Color brown, non-metallic; abdominal sternum 6 with at least six pairs of moderate to long setae in female, distinct anal brushes present on male (Fig. 27) . . . . . . *Infernophilus* new genus, p. 57

5.2. *Philophuga* Motschoulsky, 1859

Philophuga Motschoulsky, 1859- 140.

Philopheuga Bates, 1883- 202.

Glycia LeConte 1851, not Chaudoir 1842.

TYPE SPECIES.- *Philophuga cyanea* Motschoulsky, 1850 (= *P. viridis* Dejean), here designated.

The diagnostic features of this genus are presented in the key. Other characteristics, common to all species of *Philophuga*, are given in the following description.

Description.- Beetles 5.5-10.0 mm in length. Color various, but at least elytra and abdominal sterna dark with a metallic blue or green sheen; antennae black with articles 1 to 3 and base of 4 pale, at least on ventral surface.

Head with eyes prominent, convex; at least a faint post-ocular pinch present. Genae variously narrowed behind, neck evident. Labrum slightly emarginate medially; Clypeus with a single seta on each side. Frons with indistinctly defined, rugose frontal furrows; punctate, at

least laterally and posteriorly. Antennal articles 1 to 3 and base of 4 glabrous or very sparsely and finely hairy; remaining articles pubescent. Maxillary palpus with fusiform terminal article. Labial palpus with penultimate article bisetose; terminal article securiform (narrower in female). Ligula bisetose. Mentum with a prominent margined tooth.

Pronotum varied in shape; sides usually evidently sinuate behind; disc transversely rugose, best developed laterally; posterior lateral setae present or absent.

Tarsal articles glabrous or sparsely hairy above, moderately setose beneath; article 4 emarginate; claws pectinate; male with articles 1 to 4 of front and middle tarsi bearing two rows of scales beneath.

Elytra completely margined basally and apically. Hind wings full or reduced.

Abdominal sterna 3 to 5 with a pair of medial setae; sternum 6 with one to four pair of anal setae (male with usually one less pair of setae than female); sterna 4 to 6 without long lateral setae.

Male genitalia on right side in repose, left paramere large; aedeagus tube-like, with apical orifice opening slightly to left of mid-line of aedeagus; endophallus unarmed.

Female styli of typical callidine form.

Discussion.- Some members of this genus are superficially very similar to certain of the species included in the genus *Callida* (for example *Philophuga viridis amoena* LeConte and *Callida purpurea* Say; and *Philophuga brachinoides* Bates and *Callida decora* Fab.), and can often be recognized only on the basis of the character presented in the key. Even in the structure of tarsal article 4, *C. purpurea* very closely approaches the condition found in members of *Philophuga*. Perhaps when the species of

Callida are studied in more detail, it will be found necessary to include Philophuga in Callida, as a subgenus (a parallel situation occurs in the two subgenera of Plochionus Weidemann which are separated by differences in the structure of tarsal article 4). However, in this study the status of Philophuga as a distinct genus is maintained.

Distribution.- The species of Philophuga occur in the semi-arid and arid regions of Western North America.

5.2.1. Key to the species of Philophuga Motschoulsky

1. Pronotum rufous, contrasting with black head . . . . brachinoides Bates, p. 31

1'. Pronotum and head concolorous, black with a metallic blue or green sheen 2

2(1). Hind wings constantly full, membranous areas distinctly pigmented (Fig. 23); hind angle of pronotum with a setiferous puncture . . 3

2'. Hind wings reduced, without reflexed apex, or if full, membranous areas not or only lightly pigmented; hind angle of pronotum with or without a setiferous puncture . . . . . . viridis Dejean, p. 38

3(2). Head and pronotum with metallic green lustre, contrasting with blue elytra, or elytra also green; elytral striae shallowly impressed; intervals flat, finely punctate . viridicollis LeConte, p. 32

3'. Head and pronotum with metallic blue or blue-green lustre, similar in color to elytra and not contrasting; elytral striae deeply impressed; intervals convex, finely to moderately coarsely punctate . . . . caerulea Casey, p. 36

5.2.2. Philophuga brachinoides Bates, 1883

Philopheuga brachinoides Bates, 1883- 202. TYPE LOCALITY.- Cerro de Plumas, Veracruz (Selander and Vaurie, 1962), Mexico. Blackwelder, 1944- 62. (Philophuga).

Description.- Values for ratios and measurements for five specimens are: TL 6.8-7.8 mm (7.2); LE/LP 2.70-2.86 (2.75); WP/LP 1.18-1.28 (1.24); WH_1/WH_2 1.41-1.48 (1.45).

Color of prothorax, mesothorax, femora and antennal articles 1 to 3 and base of 4 rufous; remainder of body piceous to black with a metallic blue lustre.

Microsculpture obsolete on frons and disc of pronotum; strong on elytra, isodiametric medially, slightly stretched laterally.

Eyes prominent; post-ocular pinch faint. Genae strongly constricted behind, forming relatively narrow neck. Labrum broadly but shallowly emarginate. Clypeus micropunctate. Frons smooth and shiny medially, deeply but sparsely punctate posteriorly and laterally; frontal furrows short, deep, confluently punctate.

Prothorax (Fig. 33) rounded laterally, sinuate before prominent though obtuse hind angles; front angles rounded, not or only slightly protruding; hind angle on each side bearing a setiferous puncture; disc glabrous, transversely rugose. Prosternum with very short fine setae. Metasternum with scattered moderately long fine setae.

Elytral striae clearly impressed medially on disc, effaced apically and in some specimens also laterally; discal striae finely punctate, punctures coarser basally and laterally; intervals slightly convex, each bearing an irregular row of fine punctures. Wings full, strongly pigmented.

Abdominal sternum 2 with a small medial patch of setae; remaining sterna with very short sparse setae; abdominal sternum 6 with two pairs of anal setae in male, and three pairs in female.

Aedeagus elongate, slender. Female stylus as in Fig. 54.

Discussion.- This species very closely resembles Callida decora Fab. in color. It is the only species of Philophuga with pale legs and thorax.

Distribution.- I have seen only five specimens of this species from the following locality (Fig. 60).

MEXICO, Oaxaca, Rte. 190, 21.7 mi. se. Nochixtlan. 7200'. March 24, 1966 (Ball and Whitehead, UASM).

5.2.3. Philophuga viridicollis LeConte, 1848

Cymindis viridicollis LeConte, 1848- 188. LECTOTYPE.- (here selected) female, labelled as follows:- green disc, Glycia viridicollis Lec., Type 5821 MCZ, Philophuga viridicollis (Lec.).

Philophuga subcordata Chaudoir, 1877- 246. Holotype not seen. TYPE LOCALITY.- "Mexique".

Philophuga purpurea Chaudoir, 1877- 245, not Say, 1823.

Description.- Values for ratios and measurements of 40 specimens are: TL 7.1-9.6 mm; LE/LP 2.77-3.13 (2.98); WP/LP 1.07-1.29 (1.19); WH_1/WH_2 1.42-1.54 (1.47).

Color of head, pronotum and ventral parts of thorax and abdomen shiny metallic green or blue-green; elytra duller, blue or rarely in some specimens green; legs, epipleura and lateral portions of abdominal sterna piceous to black; antennae with articles 1 to 3 and base of 4 pale, at least on ventral side, outer articles black; palpi dark, with apex of terminal articles pale.

Microsculpture more or less effaced on head; lightly impressed and transverse on pronotum; finely granular on elytra, rarely slightly stretched.

Head with basal constriction gradual, neck evident; eyes prominent, convex. Labrum slightly emarginate. Clypeus smooth and shiny, irregularly and finely punctate; frons shiny, often with faint transverse rugae, sparsely but deeply punctate posteriorly and laterally; frontal furrows broad, poorly delimited, confluently punctate and longitudinally rugose; genae behind and below eyes with short sparse setae; labial palpus with terminal article very broadly dilated in male, less so in female.

Pronotum (Fig. 31) narrow, broadest in apical third, rounded laterally with a faint sinuation before hind angle; hind angle obtuse and somewhat rounded, bearing a setiferous puncture; front angle rounded, slightly protruding; base clearly margined, at least laterally. Prosternum and proepisternum sparsely punctate; prosternal punctures bearing very short fine setae. Metasternum punctate laterally, sparsely setose medially.

Elytra elongate, subparallel; striae fine, often only very faintly impressed apically, moderately punctate, punctures deeper and denser in basal half; intervals flat, with an irregular row of faint punctulae in each. Wings fully developed, strongly pigmented.

Abdominal sterna with fine setiferous punctures medially; abdominal sternum 6 with two pairs of anal setae in female and three pairs in male.

Male genitalia (Fig. 15) with aedeagus slightly arcuate dorsally; basal piece flattened, bent somewhat to right. Female stylus as in Fig. 51.

Variation.- No marked pattern of variation was noticed for this species. These characters were observed to vary within a single population sample: shape of the pronotum, microsculpture of frons and pronotum, and the depth of the elytral striae. The color of the head and the pronotum varies from metallic green to blue-green, but remains sufficiently green to contrast conspicuously with the blue elytra. This color contrast is lost in the few specimens that possess greenish elytra. Color, however, is the most reliable character for separating viridicollis from the markedly similar caerulea.

Discussion.- I have seen two specimens of viridicollis from the following California localities: San Francisco (Hopping, CAS); Needles (CAS). As no specimens of this species have been seen from Arizona and western New Mexico, these specimens may have been accidently mislabelled. The two species viridicollis and caerulea appear to be almost completely allopatric (see discussion under caerulea).

Notes on synonomy.- Say's (1823) original description of Callida purpurea and C. viridipennis (both originally assigned to Cymindis) stated that article 4 of the tarsus was bilobed for these two species, thereby confirming their position in Callida. However, Chaudoir (1877) applied the name purpurea Say to specimens of Philophuga viridicollis LeConte, and relegated the name viridicollis LeConte to synonymy. Horn (1882), after receiving identified specimens of Philophuga from Chaudoir, noticed this confusion and corrected it by placing purpurea Say in the genus Callida, and reinstating viridicollis in Philophuga. In the same paper, Horn suggested that subcordata Chaudoir was probably a synonym for viridicollis LeConte. Leng (1920) followed Horn's suggested synonymy, and although the type of subcordata Chaudoir has not been seen in this study, this synonymy is followed here.

Specimens of the species viridicollis LeConte and caerulea Casey have been confused with one another. LeConte's collection contains specimens of both of these species under the name viridicollis.

Distribution.- The species viridicollis is found in the southern Great Plains, from Kansas and eastern Colorado south into eastern New Mexico, Texas (excluding the Edwards Plateau), northeastern Mexico and possibly California - but see above (Fig. 58). I have examined over 260 specimens of this species from the following localities:-

UNITED STATES

ALABAMA: one specimen labelled "Ala." (WUM).

COLORADO: Otero Co., Rocky Ford (Hamilton, USNM).

KANSAS: Ellsworth Co., (Martin, KUM); Kiowa Co., (Woodruff, KUM); Reno Co., (Hopping, CAS); Sumner Co., (USNM).

NEW MEXICO: Lincoln Co., Ramon (Ball, UASM); Roosevelt Co., Portales (IUM), Water Canyon (Shaw, CU).

OKLAHOMA: Oklahoma Co., Oklahoma City (Grant, CAS), Stillwater (Whitaker, MCZ).

TEXAS: Atascosa Co., Plesanton (White, CNHM); Bee Co., Beeville (Tucker, USNM); Bexar Co., San Antonio (CAS, CUM, USNM); Blanco Co., Cypress Mill (USNM); Brewster Co., Alpine (CAS, USNM), Big Bend Nat'l Park (Becker & Howden, CNC), Horse Canyon (Becker & Howden, CNC), Marathon (Malkin, CNHM); Brooks Co., Falfurrias (Beer, Martin, CAS, KUM); Cameron Co., Brownsville (Glick, USNM), Bruni (Martin, CAS); Childress Co., Childress (Mitchell, USNM); Comal Co., New Braunfels (CAS, MCZ, USNM);

Culberson Co., Van Horn (Barr, IUM); Denton Co., Denton (Bishop, USNM; Duval Co., San Diego (USNM); Frio Co., Pearsall (Tucker, USNM); Hardeman Co., Quanah (Morrill, USNM); Hemphill Co., Canadian (Mann, USNM); Hidalgo Co., Edinburg (CUM, USNM); Jeff Davis Co., Davis Mts. (CAS), Ft. Davis (Ball, CAS, UAM); Karnes Co., Kenedy (Marlatt, USNM); Kerr Co., Kerrville (Becker & Howden, CNC); Kleberg Co., Kingsville (Reed, CUM); LaSalle Co., Cotulla (USNM); Lubbock Co., (Manis, IUM); Nueces Co., Corpus Christi (CNHM, USNM); Presidio Co., Marfa (Scullen, Wickham, MCZ, OUM, USNM); Randall Co., Canyon (Stephenson, KUM); Terrell Co., Dryden (Ball, UASM), Sanderson (Martin, Mason, CAS, CNC); Travis Co., Austin (Darlington, Martin, Pinkus, CAS, MCZ, USNM); Uvalde Co., Sabinal (Pratt, USNM), Uvalde (CAS, CNC, USNM); Val Verde Co., Comstock (Barr, IUM), Del Rio (CAS, CNC, USNM), Devils River (Schwarz, USNM); Victoria Co., Victoria (USNM); Ward Co., Monahans (Larson, UASM); Webb Co., Laredo (Martin, Werner, CAS, UASM).

5.2.4. Philophuga caerulea Casey, 1913

Philophuga caerulea Casey, 1913- 174. HOLOTYPE.- female labelled as follows: Ariz, Casey bequest 1925, Type USNM 47668, caerulea Casey.

Calleida viridis Chevrolat, 1835- 155. (not Dejean, 1831) TYPE LOCALITY - Las Vigas, Veracruz, Mexico.

Description.- Values for ratios and measurements for ten specimens from Arizona are: TL 7.46-9.02 mm (8.36 mm); LE/LP 2.73-3.07 (2.94); WP/LP 1.12-1.26 (1.18); WH_1/WH_2 1.44-1.57 (1.49).

Color of dorsal surface uniformly metallic blue or greenish-blue; head and pronotum more shining than elytra but of about the same hue; epipleura rufo-piceous; legs piceous to black; antennal articles 1 to 3 and base of 4 pale, at least on ventral side, outer articles black; palpi dark with apex of terminal articles paler.

Microsculpture obsolete on frons and disc of pronotum; on elytra isodiametric and finely granular medially, slightly stretched laterally.

Head as in viridicollis; short sparse setae present on genae behind and below eyes.

Pronotum (Fig. 32) varied in shape with seta present near each hind angle. More constricted basally than in specimens of viridicollis, with a longer more evident lateral sinuation; posterior lateral impressions slightly broader; lateral reflexion narrower.

Elytral striae clearly impressed, moderately punctate; intervals slightly convex, distinctly punctate, punctures stronger than in viridicollis. Hind wings fully developed; distinctly pigmented (Fig. 23).

Male genitalia as in Fig. 16. Female stylus similar to that of viridicollis.

Variation.- Size was the only character observed to vary geographically. Specimens from the southeastern portion of the range of caerulea tend to be noticably smaller than specimens from other populations. The mean length for a sample of five specimens from Las Vigas, Veracruz, was 6.92 mm (range 6.74-7.22 mm), while the mean of a sample of ten specimens from Arizona was 8.36 mm (range 7.46-9.02 mm). Too few specimens from intermediate localities were available to determine if this variation was clinal.

Discussion.- Philophuga caerulea strongly resembles viridicollis, and differs little from this species aside from the characters presented in the key. In the United States, these two species are allopatric and are readily separated from one another. However, in Mexico the distributions are too incompletely known to determine if this geographical separation is maintained. A specimen from Monterrey, and two specimens

from Monclova, Mexica, resemble viridicollis in color, but caerulea in the convexity of the elytral intervals and the depth of the striae. Perhaps when more specimens are available from Mexico, it will be necessary to treat these two species as well marked subspecies.

Distribution.- I have examined 92 specimens of this species from the following localities (Fig. 58):-

MEXICO

AQUASCALIENTES: Aquascalientes (Hendrichs).

CHIHUAHUA: Chihuahua (Wickham, MCZ).

COAHUILA: Monclova (Schwarz, USNM).

JALISCO: Guadalajara (MCZ, UASM).

MEXICO: Lerma (Ball, UASM); Presa del Angulo (Hendrichs); Toluca (Bowditch, MCZ); Valle de Bravo (Hendrichs).

NUEVO LEON: Monterrey.

PUEBLA: Tlachichuca (Ball, UASM).

TAMAULIPAS: "Mesa Gonzales" (= Gonzales?) (CAS).

VERACRUZ: Las Vigas (Hoege, MCZ, USNM).

ZACATECAS: Sombrerete (Evans, UASM).

UNITED STATED

ARIZONA: Cochise Co., Huachuca Mts. (CAS, USNM); Tombstone (UASM); Gila Co., Pinal Mts. (USNM); Santa Cruz Co., Nogales (CAS, CNHM); Patagonia (CNHM, MCZ); Sonoita (CAS, KUM); Sta. Rita Mts. (CAS, MCZ, UASM).

5.2.5. Philophuga viridis Dejean, 1831

Cymindis viridis Dejean, 1831 - 325. TYPE LOCALITY.- California. Holotype not seen. Motschoulsky, 1859- 144 (Philophuga); Horn, 1882- 144 (Philophuga); Leng, 1920 - 67; Hatch, 1953- 157. (not Chevrolat, 1835- 155).

This is the most varied species of Philophuga, containing four well defined subspecies. Characteristics common to all subspecies of viridis are presented in the following description.

Description.- Values for ratios and measurements are presented separately under each of the following four subspecies.

Color varied, ranging from dull black with a faint metallic blue sheen to bright metallic blue or green; palpi, legs and outer antennal articles piceous to black; antennal articles 1 to 3 and base of 4 pale, at least on ventral surface.

Microsculpture varied; effaced on frons and disc of pronotum in many specimens; isodiametric or slightly transverse on elytra, faintly impressed to granular.

Dorsal surface of body glabrous or setose; frons and disc of pronotum punctate.

Pronotum varied in shape; with or without a seta near each hind angle.

Elytra relatively short, oval, with greatest width in apical half. Hind wings varied in development, with reflexed apex or reduced to a small scale; when fully developed, membranous areas only lightly pigmented

Male genitalia with aedeagus short, slightly arcuate; basal piece curved (Fig. 17).

Female stylus as in Figs 52 and 53.

Geographical variation and subspecies.- The species Philophuga viridis Dejean ranges widely in the semi-arid and cold desert regions of Western North America; from the prairies of Southern Canada west to Washington and Oregon, and south to Northern New Mexico, Arizona, and

California. Over this range, color, vestiture, wing development, and the presence of the posterior-lateral prothoracic setae vary. Data on variation in these characters is summarized in a pie diagram map (Fig. 1) and in Table 2. Four subspecies are recognized, based on variation in these characters.

On the eastern side of the Rocky Mountains, and in British Columbia, Washington, and northern Oregon, populations possessing the following characteristics occur: the posterior-lateral setae of the prothorax are absent; the wings are fully developed; the dorsal surface of the body is glabrous; and the color is a dark blue-black. Associated with the absence of the posterior-lateral setae, the pronotum tends to be less sinuate laterally, with more obtuse hind angles than in specimens that possess the setae. The name <u>viridis amoena</u> LeConte applies to specimens with these characteristics.

To the west of the Rocky Mountains, a population centering around the Great Basin occurs. This subspecies, <u>v. horni</u> Chaudoir, differs from the neighboring <u>v. amoena</u> by possessing a posterior-lateral seta on each hind angle of the pronotum, and by being bright metallic green or blue in color. The hind angles of the pronotum are more distinct than in <u>v. amoena</u> and the lateral margins are more sinuate posteriorly.

Although <u>amoena</u> and <u>horni</u> are consistant in their characters over the major portion of their respective ranges, two areas of intergradation occur; along the Rocky Mountains, and in the northwestern states. In the Rocky Mountains intergradation is most pronounced around low passes. I have seen two typical specimens of <u>amoena</u> from Pocatello and Salmon, Idaho. A specimen from Dubois was colored like <u>horni</u> but lacked the posterior-lateral prothoracic setae. All other specimens seen from Idaho

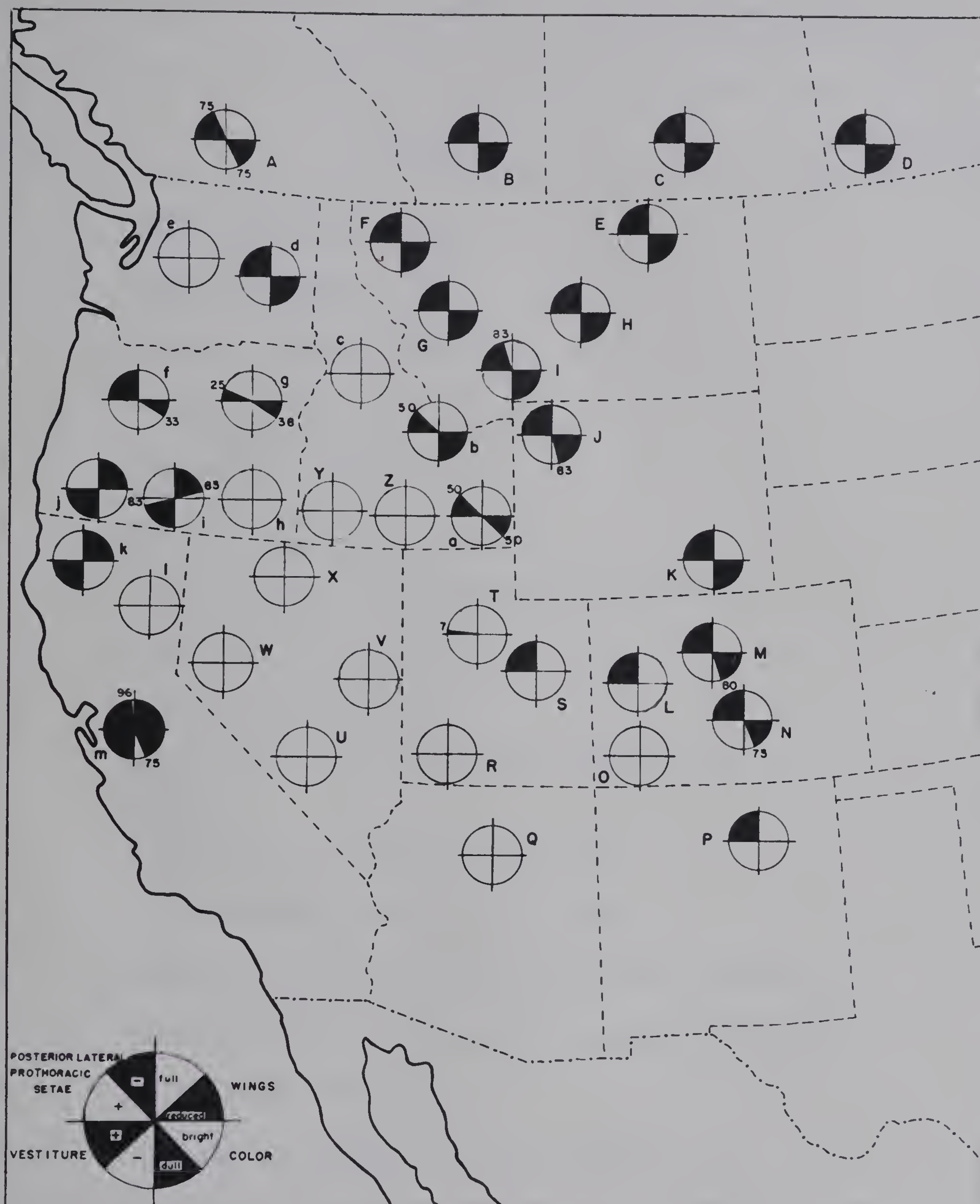


Fig. 1. Pie-diagram map illustrating geographic variation in four characteristics: wing development; color; vestiture; and presence of posterior-lateral prothoracic setae, of selected population samples of Philophuga viridis Dejean. A number external to a quadrant, indicates the percentage of specimens of that sample that show the black phase of the character. Localities represented by each pie-diagram are listed in Table 2.

Table 2. List of localities from which specimens of Philophuga viridis Dejean were used to compile pie-diagram map (Fig. 1).

Map symbol	Locality	No. of specimens
A	Southern British Columbia	4
B	Southern Alberta	24
C	Southern Saskatchewan	3
D	Southern Manitoba	15
E	Valley Co., Montana	1
F	Lake Co., Montana	1
G	Lewis & Clark, and Missoula Cos., Montana	11
H	Musselshell Co., Montana	1
I	Gallatin Co., Montana	6
J	Bighorn Co., and Yellowstone National Park, Wyoming	6
K	Carbon and Laramie Cos., Wyoming	4
L	Delta and Garfield Cos., Colorado	2
M	Boulder, Jefferson, and Larimer Cos., Colorado	5
N	Chaffee, El Paso, Park and Teller Cos., Colorado	8
O	La Plata Co., Colorado	2
P	Sapello, San Miguel Co., New Mexico	1
Q	Coconino Co., Arizona	7
R	Washington Co., Utah	1
S	Soldier Summit, Utah Co., Utah	1
T	Touele Co., Utah	12
U	Esmeralda Co., Nevada	2
V	White Pine Co., Nevada	1

Table 2 (cont'd)

Map symbol	Locality	No. of specimens
W	Washoe Co., Nevada	13
X	Humbolt Co., Nevada	1
Y	Ada, Canyon, Owyhee, and Payette Cos., Idaho	8
Z	Blaine, Cassia, Lincoln, Twin Falls Cos., Idaho	13
a	Bannock and Lake Cos., Idaho	2
b	Clark and Lemhi Cos., Idaho	2
c	Adams and Nez Perce Cos., Idaho	4
d	Grant Co., Washington	3
e	Seattle, Washington	2
f	Wasco Co., Oregon	3
g	Baker Co., Oregon	16
h	Harney, Lake, and Malheur Cos., Oregon	10
i	Klamath Co., Oregon	5
j	Jackson Co., Oregon	3
k	Yreka, California	1
l	Lassen, and Modoc Cos., California	8
m	San Francisco, California	96
	TOTAL	308

were typical horni. Some specimens from the eastern side of the continental divide in southwestern Montana and northwestern Wyoming show horni characteristics. One of the six specimens seen from Gallatin Co., Montana, possessed posterior-lateral pronotal setae. One specimen of the six seen from Yellowstone National Park had the coloration of horni.

A similar situation in which the mountains do not form a complete barrier to genetic interchange, occurs in western Colorado and eastern Utah. On the eastern slopes of the Rocky Mountains in Colorado, some specimens of amoena show a brighter metallic blue or green coloration, most obvious along the frontal grooves of the head and the lateral margins of the prothorax. Specimens from localities to the south and west in Colorado show a higher incidence of bright coloration until all specimens seen from Utah, Arizona and New Mexico show the horni coloration. The posterior-lateral prothoracic setae tend to be absent from populations of horni colored beetles in eastern Utah, western Colorado and in New Mexico. Some specimens of horni from as far west as Salt Lake City, Utah, lack these setae even though the pronotum has the characteristic shape for horni. In this region, the bright coloration of horni seems to pass through or around the southern Rocky Mountains and occurs with limited frequencies in populations on the eastern slopes of the mountains. The amoena characteristic, the absence of the posterior-lateral pronotal setae, tends to occur in populations of horni as far west as Touele Co., Utah.

The situation in the northwestern states is similar. The subspecies amoena is found in the north and western portions of Washington and Oregon. One of the four specimens I have seen from southern British Columbia is typical horni while the remaining specimens are amoena.

Even more surprising are two specimens of horni labelled Seattle, Washington (O.B.J.), while all other Washington specimens may be assigned to amoena. On the validity of O. B. Johnson's labels, Hatch (1950 : 21) stated "But if he (O. B. Johnson) believed that a given species occurred in the vicinity of Seattle, he would not hesitate, according to Professor Kincaid, to put a Seattle label on any specimen that came to hand regardless of its exact point of origin." However, a specimen with horni characteristics from southern British Columbia does not permit me to discount the possibility that horni does occur in the Seattle region. Hybrid specimens have been seen from Baker and Wasco Counties, Oregon.

The separation of amoena and horni may be primarily ecological. Specimens of amoena are found on short-grass prairie in southern Alberta, and seem to occur in regions where grassland is prevalent. The subspecies horni seems to be found in regions of desert scrub vegetation.

The third subspecies, v. klamathea new subspecies, is known from only a small area in south-central Oregon and northern California. In coloration and the shape of the pronotum (the posterior-lateral setae are present), this subspecies resembles horni. However, it is readily distinguished from the latter by the presence of sparse vestiture on the dorsal surface of the body and by the reduced hind wings which are represented by no more than small scales. On the basis of these two characters, klamathea is quite distinct from horni. Nevertheless some introgression does occur. One macropterous specimen was collected along with four micropterous beetles in a series from Klamath Co., Oregon. All specimens from the neighboring Lake Co. to the east are macropterous but some specimens show traces of fine vestiture on the elytral intervals and on the genae below the eyes (such specimens have been scored as being

glabrous in pie-graph map (Fig. 1). The subspecies klamathea does not show any signs of intergrading with amoena to the north.

The fourth subspecies, v. viridis Dejean, appears to be isolated in the vicinity of San Francisco Bay and Sonoma Co., California. Its characteristics are: hind wings reduced to a small scale; vestiture present on dorsum; color black to dull blue-black, rarely bright blue or green; posterior-lateral setae of pronotum absent from most specimens (94%), however, the lateral margin of the thorax is sinuate and the hind angles are distinct though obtuse. The basal border of the elytra tends to be more sinuate internally in micropterous than in macropterous specimens. Also, this sinuation is usually stronger in viridis s. str. than in klamathea. These two subspecies also differ in some characteristics of the elytral striae and microsculpture. These differences are described below.

The geographically isolated position of v. viridis in conjunction with the differences mentioned above, suggest that viridis and klamathea may actually be specifically distinct. However, some instability in the diagnostic characters of color and the presence of the posterior-lateral pronotal setae cause me to consider these populations to be conspecific, at least until better evidence to the contrary is discovered.

Key to the subspecies of Philophuga viridis Dejean

1. Hind wing reduced, much shorter and narrower than a single elytron 2

1'. Hind wing full, with reflexed apex 3

2(1). Hind angle of pronotum lacking setiferous puncture in most specimens (Fig. 37); elytral striae finely impressed, outer striae often obsolete and represented by a row of fine punctures . . . . v. viridis Dejean, p. 47

2'. Hind angle of pronotum with a setiferous puncture (Fig. 36); elytral striae clearly impressed, outer striae distinct almost to apex . . . . v. klamathea new subspecies, p. 48

3(2). Hind angle of pronotum with a setiferous puncture (Fig. 35) . . . . v. horni Chaudoir, p. 50

3'. Hind angle of pronotum without a setiferous puncture (Fig. 34) . . . . v. amoena LeConte, p. 53

Philophuga viridis viridis Dejean, 1831

Cymindis viridis Dejean, 1831- 325. TYPE LOCALITY.- California. Type specimen not seen. (not Chevrolat, 1835- 155).

Callida cyanea Motschoulsky, 1850- 36. TYPE LOCALITY.- San Francisco, California. Type specimen not seen.

Philophuga lauta Casey, 1913- 175. HOLOTYPE.- male, labelled as follows: Cal., Casey bequest 1925, Type USNM 47670, lauta Csy. NEW SYNONYMY.

Description.- Values for ratios and measurments of fifty-two specimens are: TL 5.7-7.5 mm (6.8 mm); LE/LP 2.39-2.80 (2.59); WP/LP 1.10-1.29 (1.21); WH_1/WH_2 1.41-1.54 (1.46).

Color dark, ranging from dull black to metallic blue or green; palpi and legs dark piceous to black; abdomen piceous to black.

Microsculpture varied; isodiametric to slightly transverse on frons, obsolete in many specimens; on disc of pronotum lightly impressed, transverse; isodiametric, faintly impressed to granular on elytra.

Body setose dorsally; evident setae present on frons behind and below eyes, on disc of pronotum and on at least odd numbered elytral intervals.

Head broad, genae broadly rounded laterally; postocular pinch faint; frons with setiferous punctures best developed posteriorly and laterally, also micropunctate.

Pronotum varied (Fig. 37); lateral margins rounded, each with a long sinuate posterior constriction; sides subparallel or slightly converging behind; front angles rounded, slightly protruding; hind angles prominent but obtuse; most specimens without posterior lateral setae (setae present in 6% of specimens examined); lateral margin narrow, widening toward hind angles; disc with sparse setiferous punctures, deeper and denser posteriorly and laterally.

Elytra relatively short, oval, with greatest width in apical half; shoulders broadly rounded, basal margin with strong anterior convexity; striae lightly impressed, finely punctae, outer striae often incomplete before apex, stria 8 represented by a row of punctures in many specimens; intervals flat to slightly convex, with an irregular row of small punctures in each. Hind wings reduced, represented by a small scale.

Abdominal sterna sparsely and finely setose; sternum 6 bearing one pair of anal setae in the male or two pairs in the female.

Male genitalia (Fig. 17) with aedeagus short, apex short; basal piece strongly curved.

Female stylus as in Fig. 52.

Distribution.- Localities from which specimens of this subspecies have been collected are indicated in Fig. 59. I have examined 96 specimens of this subspecies from the following localities:-

CALIFORNIA: Alamede Co., Grizzly Peak (Van Dyke, CAS); San Francisco Co., Lake Merced (Van Dyke, CAS), San Bruno Hills (Van Dyke, CAS), San Francisco (Blaisdell, Van Dyke, CAS, MCZ, USNM); Sonoma Co., Eldridge (CAS, USNM).

<u>Philophuga</u> <u>viridis</u> <u>klamathea</u> new subspecies

HOLOTYPE.- male, Klamath Falls, Oregon (Van Dyke, CAS).

ALLOTYPE.- female, Medford, Oregon (USNM).

Paratypes are from the following localities:-

CALIFORNIA: "Cal." (MCZ, WUM); Siskiyou Co., Yreka (USNM).

OREGON: "Or." (USNM); Jackson Co., Ashland (Stephen, OUM), Colestine (Bishop, OUM), Medford (USNM); Klamath Co., (CNHM).

The diagnostic characteristics of this subspecies are presented in the Key and in the discussion of variation under Philophuga viridis.

Description.- Values for ratios and measurements of ten specimens are: TL 6.56-8.00 mm (7.03 mm); WP/LP 1.16-1.29 (1.22); WH_1/WH_2 1.37-1.50 (1.45).

Color bright metallic blue or green. Antennal articles 1 to 3 and base of 4 pale, outer articles black.

Microsculpture highly effaced on head and pronotum making these portions shiny; irregularly isodiametric or faintly stretched on elytra, lightly impressed and shiny in many specimens.

Body setose dorsally. Setae evident on head behind and below eyes; on disc of pronotum most conspicuous along posterior-lateral margins; on disc of elytra forming an irregular row in at least odd numbered intervals. Ventral portions of body also with short evident setae.

Shape of head similar to v. horni; eyes convex, neck evidently constricted.

Pronotum as in Fig. 36, but in some specimens somewhat narrower with sides more strongly constricted behind; differing from v. viridis by being narrower with greater lateral sinuation; posterior-lateral angles each bearing a setiferous puncture.

Elytra oval, narrowed basally; basal margin strongly sinuate; striae clearly impressed on disc, outer striae evident almost to apex, strongly punctate; intervals varied, flat to convex, deeply punctate.

Male genitalia similar in shape to that of v. viridis. Female stylus as in Fig. 53.

Variation.- The following characteristics were observed to vary: shape of pronotum; density of vestiture; microsculpture, and depth of impression of elytral striae. As few specimens of this subspecies were available, I was unable to determine the pattern of variation in any of these characters. Variation was most evident among specimens from localities near the periphery of the range of klamathea, indicating that hybridization with horni may in part at least be responsible for this variation.

Relationships.- This subspecies is intermediate between viridis s. str. and horni in the diagnostic characters presented in Fig. 1. However, on the basis of its peculiar combination of characteristics, and the apparently isolated geographical position it occupies, I chose to recognize this form as a subspecies.

Etymology.- This name is the latinized form of part of the name of the type locality - Klamath Falls, Oregon.

Disposition of type material.- The holotype has been deposited in the California Academy of Sciences. The allotype is in the United States National Museum. Paratypes have been deposited in the Chicago Natural History Museum (4 specimens), Museum of Comparative Zoology (1), Oregon State University (2), United States National Museum (2) and the University of Washington (3).

Distribution.- Philophuga viridis klamathea is known only from southwestern Oregon and northern California (Fig. 59).

Philophuga viridis horni Chaudoir, 1877 NEW COMBINATION

Philophuga horni Chaudoir, 1877- 245. TYPE LOCALITY.- Nevada.

Philophuga uteana Casey, 1924- 92. HOLOTYPE.- male, labelled as follows:

Stockton, Utah, IV/7/04, Tom Spalding, Casey bequest 1925, Type USNM 47673, uteana Csy. NEW SYNONYMY.

Philophuga cobaltina Casey, 1924- 91. HOLOTYPE.- male, labelled as follows: Trout Creek Juab Co., Utah, VII/4/22. Tom Spalding, Casey bequest 1925, Type USNM 47672, cobaltina Csy. NEW SYNONYMY.

Description.- Values for ratios and measurements of ten specimens are: TL, 7.02-8.24 mm (7.58 mm); LE/LP, 2.77-2.93 (2.83); WP/LP, 1.21-1.27 (1.24); WH_1/WH_2, 1.38-1.50 (1.45).

Color shiny metallic blue or green. Antennal articles 1 to 3 and base of 4 pale, outer articles black.

Microsculpture absent or highly effaced on head and pronotum; strong on elytra, isodiametric medially showing tendency to become stretched and arranged in transverse rows laterally.

Body glabrous dorsally; even head below eyes without setae.

Head with eyes large, strongly convex; genae constricted posteriorly forming evident neck.

Pronotum as in Fig. 35; lateral margin with long sinuation towards hind angle; hind angles prominent though somewhat obtuse, each bearing a setiferous puncture.

Elytra with greatest width in apical half but not strongly narrowed basally; basal border only slightly sinuate; elytral striae clearly impressed, moderately to coarsely punctate; intervals slightly to strongly convex, finely to coarsely punctate. Hind wings fully developed.

Male with three, female with two pair of anal setae on abdominal sternum 6.

Male genitalia similar to that of v. viridis. Female stylus as in v. klamathea.

Distribution.- This subspecies occurs throughout the Great Basin province, and extends a little outside of this region especially in the north (Fig. 59). I have seen more than 90 specimens from the following localities:-

UNITED STATES

ARIZONA: Coconino Co., Flagstaff (USNM), Pinal Mts. (CU), Williams (Wickham, USNM).

CALIFORNIA: Lassen Co., Bridgeport (Wickham, USNM), Hallelujah Junction (Westcott, UASM), Susanville (Martin, CAS); Modoc Co., Davis Creek (Fox, CAS), Hackmore (Van Dyke, CAS).

COLORADO: La Plata Co., Pagosa Springs (Bowditch, MCZ).

IDAHO: Ada Co., Nampa (Barr, IUM), Regina (Barr, IUM); Adams Co., Martin (Houk, WUM), Mesa (IUM); Bear Lake Co., Bear Lake (AMNH); Blaine Co., Carey (Hewitt, IUM), Crystal Ice Cave (Westcott, IUM), Magic Reservoir (Barr, IUM); Canyon Co., Caldwell (Barr, IUM), Parma (WUM); Cassia Co., Elba-Basin Pass (Stecker, SJSC), Malta (Henry, IUM), Rupert (Shull, IUM); Clark Co., Dubois (Penrose, UASM); Lincoln Co., Richfield (Barr, IUM); Nez Perce Co., Lewiston (Shull, IUM, USNM); Owyhee Co., Bruneau (Fillmore, IUM), Jordan Valley (Henry, IUM), Reynolds (Hewitt, IUM); Payette Co., Payette (Shull, IUM); Twin Falls Co., Hollister (Fox, USNM), Twin Falls (Homan, IUM).

NEVADA: Esmeralda Co., Lida (O'Brien, UASM); Humbolt Co., Winnemucca (Barr, IUM); Washoe Co., Reno (Wickham, CAS, MCZ, USNM), Steamboat Springs (Van Dyke, CAS), Verdi (Blaisdell, CAS); White Pine Co., Ely (Van Dyke, CAS).

OREGON: Baker Co., Baker (Van Dyke, CAS, WUM), Durkee (WUM), Pleasant Valley (Fender, WUM), Sparta (Van Dyke, CAS), Wallowa Mts.

(Van Dyke, CAS); Harney Co., Frenchglen (Malkin, WUM), Tencent Lake (Malkin, CNHM, WUM); Lake Co., Hart Mtn.. Antelope Refuge (Nelson, OUM); Malheur Co., Harper (OUM), Rome (CAS, OUM).

NEW MEXICO: San Miguel Co., Sapello (Ball, UASM).

UTAH: Tolle Co., Stanisbury I. (USNM), Stockton (Spalding, CAS, MCZ); Utah Co., American Fork (H&S, USNM); Washington Co., St. George (AMNH).

WASHINGTON: King Co., Seattle (O.B.J., WUM).

Philophuga viridis amoena LeConte, 1848 NEW COMBINATION

Cymindis amoena LeConte, 1848- 188. LECTOTYPE.- (here selected) female, labelled as follows: green disc, amoena LeC., Type 5822 MCZ, P. amoena (LeC.).

Philophuga canora Casey, 1913- 174. HOLOTYPE.- female, labelled as follows: Tex., Casey bequest 1925, Type USNM 47669, canora Csy. NEW SYNONYMY.

Philophuga puella Casey, 1913- 176. HOLOTYPE.- male, labelled as follows: Boulder Co., Colo., Casey bequest 1925, Type USNM 47671, puella Csy. NEW SYNONYMY.

Philophuga obscura Casey, 1924- 91. HOLOTYPE.- female, labelled as follows: N.Y., Casey bequest 1925, Type USNM 47674, obscura Csy. NEW SYNONYMY.

Description.- Values for ratios and measurements of ten specimens are: TL 7.20-8.32 mm (7.52 mm); LE/LP, 2.68-2.90 (2.80); WP/LP, 1.18-1.24 (1.21); WH_1/WH_2, 1.28-1.46 (1.40).

Color black (elytra piceous in some specimens) with a dull metallic blue sheen on disc of pronotum and elytra; very rarely with faint blue-green sheen, usually restricted to frontal furrows and lateral margins of

pronotum. Antennae with articles 1 to 3 and base of 4 pale, at least ventrally.

Body glabrous dorsally; glabrous even laterally behind and below eye.

Head broad; eyes flattened, somewhat reduced; neck broad. Antennae with outer articles relatively short and stout.

Pronotum (Fig. 39) convex; sides slightly rounded and only shallowly sinuate posteriorly; hind angles broadly rounded and lacking setiferous puncture on each side; front angles rounded, not or only slightly protruding; lateral margin narrowly and uniformly reflexed.

Elytra relatively convex, elongate oval, with greatest width in apical third; shoulders broad, basal border slightly sinuate interiorly; striae finely impressed, finely to moderately punctate; intervals faintly convex basally, flat apically, sparsely and finely punctate.

Abdominal sternum 6 with one pair of anal setae in male, and two pairs in female.

Male genitalia as in _v. viridis_.

Female stylus as in the other subspecies of _viridis_.

Variation.- Hybridization between _v. amoena_ and _v. horni_ has been discussed above. Some variation has been observed in the eastern portion of the range of _amoena_. Here, hybridization with _horni_ would not occur.

Only a single female specimen has been seen from Kansas. It differs from the more typical western and northern specimens of _amoena_ by having a greenish-blue cast dorsally, and by possessing a strongly rounded pronotum with a strong lateral reflexion, narrow anteriorly and broadening behind.

The single female specimen seen from Nebraska has a normally proportioned pronotum, but the elytral striae are rather coarsely punctate, and the elytral intervals are convex and coarsely punctate.

Distribution.- This species occurs primarily on the Great Plains east of the Rocky Mountains, and along the northern periphery of the Great Basin (Fig. 59).

CANADA

ALBERTA: Lethbridge (Larson, UASM); Lost River nr. Onefour (Larson, UASM); Medicine Hat (Carr, Pepper, CAS, CNC, CU, UASM); Milk River (Pepper, CNC); Ralston (Ball, UASM); Taber (White, DAL).

BRITISH COLUMBIA: Mts. between Hope and Okanagan (Bowditch, MCZ); "Van." (= Vancouver ?) (MCZ).

MANITOBA: Aweme (Criddle, White, AMNH, CAS, CNC, CU, DAL, USNM); Brandon (AMNH, USNM).

SASKATCHEWAN: Cypress Hills (Ball & Lindroth, UASM); Roche Percee (Criddle, CNC); Saskatoon (McMillan, CNC).

UNITED STATES

COLORADO: Boulder Co., Nederland (Stainer, CNC); Chaffee Co., Buena Vista (Wickham, USNM); Delta Co., Paonia (Van Dyke, CAS); El Paso Co., Colorado Springs (Soltau, Wickham, MCZ, USNM); Garfield Co., Glenwood Springs (AMNH); Jefferson Co., Denver (Soltau, USNM); Mesa Co., Grand Junction (Titus, USNM); Park Co., Trout Creek Pass (Beamer, KUM), Wilkerson Pass (White, KUM); Teller Co., Florissant (Bowditch, MCZ).

IDAHO: Bannock Co., Pocatello (Bruner, USNM); Lemhi Co., Salmon (Wakeland, IUM).

KANSAS: "Ks." (MCZ).

MONTANA: Gallatin Co., Bozeman (WUM), Gallatin Co., (MUB); Lake Co., (MUB); Lewis and Clark Co., Helena (many collectors, CAS, MCZ, USNM); Missoula Co., Missoula (MUB); Musselshell Co., (MUB); Valley Co., Hinsdale (MUB).

NEBRASKA: "Neb." (MCZ).

OREGON: Wasco Co., Maupin (Van Dyke, CAS), Warm Springs Indian Reserve (WUM).

WASHINGTON: Grant Co., Dry Falls (Burnes, WUM), Grand Coulee (MCZ), Soap Lake (Hatch, WUM).

WYOMING: Bighorn Co., Bighorn Mts. (Edwards, SJSC); Carbon Co., Rawlins (AMNH); Laramie Co., Chyenne (Soltau, USNM); Yellowstone National Park (Hatch, Van Dyke, CAS, WUM).

5.3. Infernophilus new genus

TYPE SPECIES.- Philophuga castanea Horn, 1882; here designated.

The species I. castaneus Horn was described originally as a member of the genus Philophuga, but it differs in several important details from the other species included in that genus. Further, this species cannot be included in any other known callidine genus. For these reasons, the genus Infernophilus is established to include castaneus.

The most striking external features of this genus are indicated in the preceding key. Another remarkable feature is the orientation of the male genitalia. In repose, the aedeagus is on its left instead of on its right side; the latter is the usual position among the members of the Lebiini. Associated with this, the parameres are reversed. They are of the typical form for the Callidina, but the large paramere is on the right rather than on the left side of the aedeagus. Also, the apical orifice opens dorso-laterally to the right. I know of no other North American callidine, or even lebiine, that shows a similar condition. As no intermediate stages are known between the normal and the reversed position of the genitalia, it seems plausible that the initial 180^{o} rotation arose in a single step. Other modifications such as the reversal of the parameres and the shift of the apical orifice may have been secondary.

Etymology.- The name is derived from the Latin noun infernus - m., hell; and the Greek philia - fondness. The name refers to the hot desert region in which this insect is found.

5.3.1. Infernophilus castaneus Horn, 1882

Philophuga castanea Horn, 1882- 144. TYPE LOCALITY.- Kern Co., California.

Leng, 1920- 67. Csiki, 1932- 1462.

Description.- Values for ratios and measurements for fourteen specimens are: TL 7.9-9.1 mm (8.6 mm); LE/LP 2.62-2.84 (2.74); WP/LP 1.07-1.25 (1.17); WH_1/WH_2 1.46-1.56 (1.52).

Color brown; elytra and abdomen darker brown to piceous.

Microsculpture on frons isodiametric, but effaced on most specimens; obsolete on disc of pronotum; isodiametric on elytra, but partly effaced and shiny. Body sparsely setose above.

Head with eyes prominent, convex. Genae broad behind eyes, with faint postocular pinch; narrowing posteriorly to form an evident neck. Labrum slightly emarginate. Clypeus with a single seta on each side; sparsely punctulate medially. Frons with poorly defined rugose frontal furrows; sparsely punctate medially with deeper setiferous punctures posteriorly and laterally. Antennae with articles 1 to 3 and base of 4 sparsely hairy; remaining articles pubescent. Maxillary palpus with terminal article cylindrical. Labial palpus with penultimate article bisetose; terminal article securiform (narrower in female). Ligula bisetose. Mentum with a prominent margined tooth.

Pronotum (Fig. 30) varied in shape; lateral sinuation long, lateral margins subparallel toward base; hind angles obtuse, with setiferous puncture present; base slightly sinuate laterally; frontal angles broadly rounded, slightly protruding; posterior lateral impressions indistinctly limited and continuous with broad lateral grooves; lateral margins uniformly reflexed; disc transversely rugose laterally.

Tarsal articles sparsely hairy above, densely setose beneath; article 4 emarginate; basal article of middle and hind tarsi with faint median dorsal groove; claws pectinate; male with articles 1 to 3 of front tarsus and articles 1 and 2 of middle tarsus bearing two rows of scales beneath.

Elytra completely bordered both apically and basally; striae clearly impressed and well defined to apex, lightly punctate; intervals broadly convex, bearing small irregular setiferous punctures; odd-numbered intervals and apex of even numbered intervals with an irregular row of larger setiferous punctures. Hind wings fully developed.

Abdominal sternum 6 of male with a paired brush of setae along hind margin (Fig. 27); in female brush reduced and in some specimens it is represented by as few as six pairs of moderate to long setae.

Male genitalia (Figs. 21-22) with reversed parameres; endophallus with a field of short spines.

Stylus of ovipositor (Fig. 57) short, broad; broadly rounded apically, sparsely setose.

Distribution.- I have examined fifteen specimens of this species from the following localities (Fig. 61):

CALIFORNIA: Kern Co., (AMNH); Mono Co., Bridgeport (O'Brien, UAM), Coleville (O Brien, CAS, DAO, UAM); San Diego Co., (USNM). NEVADA: (AMNH, USNM).

Biology.- Several specimens in a series taken at Coleville, California (July 6-10, 1966) were slightly teneral.

5.4. Tecnophilus Chaudoir, 1877

Tecnophilus Chaudoir, 1877 240.

TYPE SPECIES.- Calleida croceicollis Menetries, 1843, here designated.

Philotecnus LeConte, 1851- 175, not Mannerheim, 1837- 42.

TYPE SPECIES.- Philotecnus nigricollis LeConte, 1851 (= T. croceicollis Menetries), here designated.

This is a small genus closely related to Philophuga. Aside from the characters presented in key 5.1., the adults can be recognized on the

basis of the cordate pronotum and the usually dense vestiture of the body.

Characteristics common to all species of Tecnophilus are given in the following description.

Description.- Beetles 5.7 to 8.0 mm in length. Color various, but elytra always metallic blue or green. Basal three articles of antenna similarly colored to outer articles.

Body variously punctate and setose dorsally; ventral portions of body moderately to densely setose.

Eyes prominent, of various convexity; hairy or glabrous. Labrum truncate apically with slight medial elevation. Frontal furrows shallow, broad, deeply punctate. Frons punctate. Antennal articles 1 to 3 and base of 4 hairy; outer articles pubescent. Maxillary palpus with fusiform terminal article. Labial palpus with terminal article securiform; penultimate article bisetose. Ligula bisetose. Mentum with a prominent margined tooth.

Pronotum cordate, with strong posterior-lateral sinuations; lateral setae present; hind angles lacking setiferous punctures.

Tarsal articles slender; article 4 at most emarginate; hairy dorsally; tarsal claws simple (in some specimens may be minutely serrulate); articles 1 to 3 of front tarsi, and 2 and 3 of middle tarsi of male bearing two rows of scales beneath.

Elytra parallel sided or oval; completely margined both basally and apically; striae evident and punctate; intervals variously punctate. Hind wings fully developed.

Abdominal sterna 3, 4 and 5 with a pair of medial setae; sternum 6 with at most three pairs of anal setae; sterna 4 to 6 without long lateral setae.

Male genitalia lying on right side in repose. Left paramere large; right paramere smaller, bilobed apically. Aedeagus simple, tube-like, with apical orifice opening somewhat laterally to the left; endophallus unarmed.

Female stylus with densely setose apex.

Discussion.- Chaudoir (1877) separated Tecnophilus from his Callides on the basis of the structure of the ligula and paraglossae, and placed the genus in his Mimodromiides. However, Horn (1881) carefully studied the ligula and paraglossae of the Lebiini and concluded that they were of little value in defining groups of higher rank than the genus, and even here he suggested that they be used with caution. Tecnophilus is certainly a callidine in the sense used here.

Many of the peculiar features of Tecnophilus, such as the simple tarsal claws, slender tarsi, cordate pronotum and setose body, may be regarded as adaptations to a terrestrial mode of life.

Distribution.- The members of this genus are found in alkaline or saline situations in western North America.

5.4.1. Key to the species of Tecnophilus Chaudoir

1. Apex of femur infuscated and contrasting with the otherwise rufous legs . . . . pilatei Chaudoir, p. 61

1'. Femur concolorous, rufous to black; or if femur rufous and infuscated apically, tarsi also infuscated . croceicollis Menetries, p. 63

5.4.2. Tecnophilus pilatei Chaudoir, 1877

Tecnophilus pilatei Chaudoir, 1877- 239. TYPE LOCALITY.- Texas. Horn, 1882- 137. Leng, 1920- 67. Csiki, 1932- 1462.

Specimens of this species can be readily recognized by possession of

the infuscated apices of otherwise rufous femora. Also, the elytral striae are much more coarsely punctate than in croceicollis.

Description.- Values for ratios and measurements of ten specimens are: LE 4.44-4.76 mm (4.56 mm); WP/LP 1.06-1.15 (1.10); WH_1/WH_2 1.61-1.70 (1.65).

Color of head and thorax rufous; abdomen piceous medially, paler laterally; elytra metallic blue or green, often with rufinistic background; antennae and palpi pale; legs pale except for conspicuous infuscated apical spot on femur.

Microsculpture obsolete on head; lightly impressed, transversely stretched on disc of pronotum; isodiametric but shallowly impressed on elytra.

Body densely pubescent, both dorsally and ventrally.

Head narrow, with temporal region strongly consticted; eyes very convex and protruding, glabrous.

Pronotum (Fig. 38) narrow; sides slightly rounded laterally, relatively shallowly sinuate behind; front angles rounded, not protruding; hind angles obtuse, broadly rounded; lateral reflexion narrow.

Tarsal article 4 deeply emarginate, almost bilobed but not bearing dense setiferous pads beneath.

Elytra elongate, parallel sided; striae moderately impressed medially on disc, becoming obsolete laterally; striae with very coarse often confluent punctures, deepest in basal half but also evident apically; intervals flat; basal margin strongly sinuate internally; apex obliquely truncate and slightly sinuate.

Abdominal sternum 6 of male with two pairs of anal setae, with three pairs in female.

Male genitalia as in Fig. 18; aedeagus slightly arcuate, apex elongate.

Female stylus (Fig. 55) with external apical angle greatly produced.

Relationships.- Specimens of the species pilatei superficially resemble Texas specimens of the species croceicollis. However, the strikingly different styli of the female ovipositor and the elongated apex of the male genitalia, associated with the external characteristics mentioned above, consistently separates specimens of these two species. The species pilatei is isolated from the croceicollis complex.

Distribution.- I have seen specimens of this species only from localities along the Gulf Coast of Texas (Fig. 62). I examined 140 specimens from the following localities:

TEXAS: Aransas Co., Goose Island State Park (Larson, UASM), Brazori Co., Freeport (Evans, UASM); Cameron Co., Brownsville (UASM. USNM), Port Isabel (Ball, UASM), Cedar Lane (Shaw, KUM); Nueces Co., Corpus Christi (Hubbard & Schwarz, USNM).

5.4.3. Tecnophilus croceicollis Menetries, 1843

Calleida croceicollis Menetries, 1843- 54. TYPE LOCALITY.- California.

The most diagnostic characteristic of this highly variable species is presented in the preceding key to the species of the genus Tecnophilus (section 5.4.1.).

Description.- Values for ratios and measurements of selected population samples are presented in Tables 6 to 10.

Color highly varied; head and pronotum black to rufous with head always same color or darker than disc of pronotum; appendages black to rufous, femur uniformly colored, or if rufous and infuscated apically, tarsus and clypeus also infuscated; elytra black to piceous with metallic green, blue or purple sheen.

Vestiture varied, but even in least setose specimens setae present on head behind and below eyes, along lateral margins of pronotum and on at least odd numbered elytral intervals; dorsal vestiture of most specimens quite conspicuous.

Microsculpture obsolete on frons; on pronotum consisting of partially effaced transverse meshes; on elytra isodiametric but shallowly impressed and shiny on many specimens.

Head with neck variously constricted; eyes of various size and convexity (Figs. 24 and 25).

Pronotum varied; more rounded laterally and more constricted behind than in pilatei (Figs. 39-42).

Elytra with basal border shallowly sinuate; apex truncate or slightly sinuate; striae finely to moderately punctate, never as coarsely punctate as in pilatei.

Aedeagus of male genitalia (Figs. 19 and 20) short, arcuate, with short apex.

Female stylus (Fig. 56) with apex truncate, not produced.

Geographical variation and subspecies.- The complex geographical variation displayed by this species makes it very difficult to organize the available population samples into well defined subspecies. Clinal variation occurs in several characteristics, and the general pattern of variation is discordant. Geographically terminal populations are comprised of individuals easily distinguished by distinctive combinations of characters, but specimens from intermediate areas are often difficult to associate with the terminal groups. However, as is shown below, it is possible to distinguish two groups of subspecific rank.

The pattern of variation of each character is described below, and this section is concluded with a summary of this information.

Color.- Over much of the range of croceicollis, the basic color pattern is as follows: elytra metallic blue or green; head, pronotum, and legs rufous; abdominal sterna piceous. However, considerable variation in color of each of these body parts occurs.

Data on variation in the color of the elytra among selected population samples of the species croceicollis are presented in Table 3. Briefly, the color of the elytra varies in the following way: populations from the vicinity of San Francisco Bay, and from the Central Valley of California, possess dark blue or purple elytra; populations from southern California, Arizona, Nevada, and southern Utah generally have blue elytra, with a very small percentage of the specimens possessing greenish-blue or green elytra. The incidence of green elytra increases southwardly along the Gulf of California, and eastwardly through New Mexico, until green or blue-green is the predominant color in Texas populations. All specimens seen from Wyoming and Alberta show dark blue elytra. West of the Rocky Mountains in Idaho and northern Utah, the color of the elytra is highly varied.

Data on variation in the color of the head and pronotum are presented in Tables 4 and 5. In specimens that show infuscation of the head and pronotum, the head is always the same color or darker than the disc of the pronotum. All specimens that have been seen from Mexico, and the United States from southeastern California east to Texas, and north to central Colorado, Utah, and Nevada, possess rufous heads and pronota. Specimens from the eastern side of the Rocky Mountains from northern

Table 3. Geographical variation in color of elytra of *Tecnophilus croceicollis* Menetries

Locality	Number of specimens	Purple	Blue	Blue-green	Green
Alberta	52	9	38	9	-
Wyoming	7	-	7	-	-
Idaho	5	1	1	2	1
San Francisco Bay, California	39	34	4	1	-
Central Valley, California	29	9	13	7	-
Cuddeback L., California	65	-	15	38	12
Arizona	32	-	13	18	-
Texas	38	-	1	12	25
Sinaloa, Mexico	8	-	-	-	8

Table 4. Geographical variation in color of head of

Tecnophilus croceicollis Menetries

Locality	Number of specimens	Black	Piceous	Rufous
Alberta	52	52	-	-
Wyoming	7	7	-	-
Idaho	5	2	3	-
San Francisco Bay, California	39	30	8	1
Central Valley, California	41	4	28	9
Cuddeback L., California	65	-	-	65
Arizona	32	-	-	32
Texas	38	-	-	38
Sinaloa, Mexico	8	-	-	8

Table 5. Geographical variation in color of pronotum of *Tecnophilus croceicollis* Menetries

Locality	Number of specimens	Black	Piceous	Rufous
Alberta	52	52	-	-
Wyoming	7	7	-	-
Idaho	5	1	1	3
San Francisco Bay, California	39	9	16	14
Central Valley, California	41	1	4	36
Cuddeback L., California	65	-	-	65
Arizona	32	-	-	32
Texas	38	-	-	38
Sinaloa, Mexico	8	-	-	8

Colorado to southern Alberta, possess black heads and pronota. I have not seen any specimens from Colorado that were intermediate between the black color of northern specimens, and the rufous color of specimens from southern localities. This suggests that no hybridization occurs between specimens belonging to these two different color classes in this region. However, west of the Rocky Mountains in Idaho and northern Utah, specimens of croceicollis are highly varied in color, with the color ranging from entirely black to rufous with only a light infuscation of the tarsi and the clypeus. This variability in color probably results from hybridization between the black members of the northern population, and rufous colored specimens which occupy the Great Basin. Similar variation in color occurs among populations in the Central Valley of California. Many specimens occurring around San Francisco Bay are black in color. Specimens from further inland tend to be paler, and specimens from the southern end of the San Joaquin Valley are almost as pale as specimens from the Mojave Desert. This evidence suggests that there is gene flow from the Mojave Desert, into the San Joaquin Valley.

Vestiture.- Specimens from southeastern Alberta, and from southeastern California and the neighboring portion of Arizona, possess very short sparse setae. Over the remainder of the range of croceicollis, specimens are moderately setose, or in southern New Mexico and along the Rio Grande in Texas, specimens are very densely setose.

Measurements and ratios.- Five measurements were taken of specimens of Tecnophilus croceicollis. Various combinations of these measurements were made up to produce four ratios to map out the general shape of the insects and to quantify observed differences in habitus between members belonging to different populations of this species. Values for

measurements and ratios of four population samples of the species croceicollis are presented in Tables 6 to 10. This data is given for only four population samples, as these four samples are the only homogeneous samples available of sufficient size to be statistically significant. The analysis of variation which follows is based on these four samples.

Below, the pattern of variation shown by each of these characters is discussed separately.

Length of elytra (Table 6).- This measurement is taken as giving an index of the size of the beetle. The largest specimens seen were from coastal localities (Brownsville, Texas, $\overline{X}$ = 4.38 mm; Newark, California, $\overline{X}$ = 4.21 mm). Specimens from intermediate inland localities were smaller (Cuddeback Lake, California, $\overline{X}$ = 4.03) and the smallest specimens seen were from northern inland localities (Lost River Ranch, Alberta, $\overline{X}$ = 3.73 mm).

Width of pronotum/length of pronotum (Table 7).- The population sample with the highest mean value for this ratio is from Newark, California ($\overline{X}$ = 1.22). The sample from Cuddeback Lake, California has the lowest mean value for this ratio ($\overline{X}$ = 1.14). Population samples from Brownsville, Texas and Lost River Ranch, Alberta possess intermediate mean values, and do not differ significantly between themselves.

Length of elytra/length of pronotum (Table 8).- The pattern of variation shown by this character is similar to the pattern of variation shown by the length of the elytra. The samples with the largest mean values are from coastal localities while samples from inland and northern localities possess smaller mean values for this ratio.

Table 6. Geographical variation in length of elytra (mm) among selected population samples of Tecnophilus croceicollis Menetries

Locality	N	Range	Mean	S.E.	S.D.	C.V.%
Newark, Cal.	40	3.83-4.57	4.21	0.03	0.20	4.75
Cuddeback L., Cal.	64	3.64-4.48	4.03	0.03	0.22	5.71
Brownsville, Texas	20	3.92-4.77	4.38	0.06	0.25	5.71
S.E. Alberta	38	3.30-4.28	3.73	0.04	0.23	6.17

Table 7. Geographical variation in the ratio width of pronotum/length of pronotum among selected population samples of Tecnophilus croceicollis Menetries

Locality	N	Range	Mean	S.E.	S.D.	C.V.%
Newark, Cal.	40	1.16-1.32	1.22	0.01	0.04	3.28
Cuddeback L., Cal.	64	1.06-1.25	1.14	0.01	0.04	3.51
Brownsville, Texas	20	1.15-1.23	1.18	0.01	0.02	1.69
S.E. Alberta	38	1.13-1.25	1.19	0.01	0.03	2.52

Width of pronotum/maximum width of head (Table 9).- The pattern of variation in this character is similar to the pattern of variation shown by the character width of pronotum/length of pronotum. The sample from Newark, California possesses the greatest mean value for this ratio ($\overline{X}$ = 1.18) while the sample from Cuddeback Lake, California has the smallest mean value ($\overline{X}$ = 1.10). The means for the samples from southeastern Alberta and from Brownsville, Texas are identical in value to one another ($\overline{X}$ = 1.14) and are intermediate between the mean values for the two California population samples.

Maximum width of head/minimum width of frons between eyes (Table 10).- The sample with the largest mean value for this ratio is from Brownsville, Texas ($\overline{X}$ = 1.63). This is followed in descending order by the samples from Cuddeback Lake, California ($\overline{X}$ = 1.54), Newark, California ($\overline{X}$ = 1.45), and southeastern Alberta ($\overline{X}$ = 1.41). The value for this ratio becomes smaller for samples from east to west and from south to north.

The above five characters show several different patterns of variation. Because it is difficult to justify the weighting of any one of these characters above the other four in any given comparison of population samples, all characters were used simultaneously to develop discriminant functions to compare population samples with one another. For each comparison of a pair of population samples, a weight was calculated for each character used. The calculation was such that the value of the weight depended upon the discriminatory value of the character in that comparison (see Stanly MS for details on calculation). That is, if a character can separate members of two populations consistently, that character has a higher weighting coefficient than a character that gives inconsistent separations.

Table 8. Geographical variation in the ratio of length of elytra/length of pronotum among selected population samples of _Tecnophilus_ _croceicollis_ Menetries

Locality	N	Range	Mean	S.E.	S.D.	C.V.%
Newark, Cal.	40	2.76-3.06	2.92	0.01	0.08	2.74
Cuddeback L., Cal.	64	2.65-3.11	2.84	0.01	0.08	2.82
Brownsville, Texas	20	2.84-3.09	2.95	0.02	0.08	2.71
S.E. Alberta	38	2.59-2.82	2.71	0.01	0.06	2.21

Table 9. Geographical variation in the ratio of width of pronotum/maximum width of head among selected population samples of _Tecnophilus_ _croceicollis_ Menetries

Locality	N	Range	Mean	S.E.	S.D.	C.V.%
Newark, Cal.	40	1.09-1.24	1.18	0.01	0.03	2.54
Cuddeback L., Cal.	64	1.03-1.16	1.10	0.01	0.04	3.64
Brownsville, Texas	20	1.08-1.20	1.14	0.01	0.03	2.63
S.E. Alberta	38	1.07-1.18	1.14	0.01	0.03	2.63

Table 10. Geographical variation in the ratio of maximum width of head/minimum width of head between eyes among selected population samples of *Tecnophilus croceicollis* Menetries

Locality	N	Range	Mean	S.E.	S.D.	C.V.%
Newark, Cal.	40	1.40-1.53	1.45	0.01	0.03	2.07
Cuddeback L., Cal.	64	1.49-1.63	1.54	0.01	0.03	1.95
Brownsville, Texas	20	1.57-1.67	1.63	0.01	0.03	1.84
S.E. Alberta	38	1.31-1.48	1.41	0.01	0.03	2.13

For the sake of brevity in the following discussion, the population samples used in the comparisons are designated alphabetically, as follows:

A = Brownsville, Texas

B = Cuddeback Lake, California

C = Newark, California

D = Lost River Ranch, Alberta

Not all possible combinations of population comparisons were made. The Brownsville, Texas population sample was not compared with the population sample from Newark, California because both of these populations were independently compared with the geographically intermediate population sample from Cuddeback Lake, California. Thus, the A versus C comparison was made indirectly. Similarly, an indirect comparison between Newark, California (C) and Lost River Ranch, Alberta (D) was made. The populations of croceicollis in the central valley of California appear to be effectively isolated to the north and east by the Klamath Mountains and Sierra Nevadas respectively. This means that any genetical connection between these two populations would have to be indirect, through southern California. For this reason, the population sample from Cuddeback Lake was also taken as being intermediate between these two populations.

Comparisons between pairs of populations were made in the following way. A $\overline{Z}_i$ value (the sum of the mean character values multiplied by their individual weighting coefficients) was calculated for each of the two population samples compared. An axis was plotted on a map joining the localities from which these population samples were obtained. Using the weighting coefficient calculated for the original comparison, $\overline{Z}_i$

values were calculated for samples from geographically intermediate localities that lay along the axis and these $\overline{Z}_i$ values were plotted on a map. Where the $\overline{Z}_i$ value obtained from geographically intermediate population samples was equal to or approached the mid-point value, a transverse line was drawn across the axis. This transverse line theoretically divided members of the two populations and their associated specimens from one another. If the position in which this transverse line occurred was concordant with a change in the state of one or more other characters such as color, the populations separated by this line were considered to be subspecifically distinct.

A summary of the population comparisons that have been made is presented below. Table 11 gives the weighting coefficients and the calculated $\overline{Z}_i$ values of the population samples used for each set of comparisons.

Brownsville, Texas versus Cuddeback Lake, California (Comparison A-B).- Calculated $\overline{Z}_i$ values for population samples from Brownsville, Texas and Cuddeback Lake, California and for specimens from intermediate localities are presented in Table 12, and are plotted on a map in Fig. 2. The line transverse to the A-B axis separates populations with $\overline{Z}_i$ values above the mid-point from populations with $\overline{Z}_i$ values below the mid-point value. This line is not concordant with that of any other character observed to vary between the two populations.

Brownsville, Texas versus Lost River Ranch, Alberta (Comparison A-D).- Calculated $\overline{Z}_i$ values for the two population samples compared and for specimens from intermediate localities are presented in Table 13 and are plotted on a map in Fig. 3. The transverse line representing the position in which mid-point values are expected to occur extends across

Table 11. Summary of calculated weighting coefficients (W^*) and $\overline{Z}_i$ values obtained for each comparison of a pair of population samples of Tecnophilus croceicollis Menetries

Comparison I	vs II	W_1	W_2	W_3	W_4	W_5	$\overline{Z}_I$	$\overline{Z}_{II}$	Mid-point Z_i value	% overlap Observed	% overlap Calculated
A	B	0.715	0.105	0.845	-0.135	-0.489	1.721	1.613	1.667	25	44
A	D	-	-0.053	3.643	1.165	-	9.102	8.090	8.596	0	30
B	C	-0.489	-0.029	0.715	0.707	0.038	0.673	0.568	0.621	8.8	44
B	D	-3.281	-0.223	2.023	1.396	3.768	6.611	6.209	6.410	0	22

W_1 to W_5 are weighting coefficients for characters X_1 to X_5 respectively, where character: X_1 = WP/LP; X_2 = LE mm; X_3 = WH_1/WH_2; X_4 = LE/LP; and X_5 = WP/WH_1.

Population samples have been designated alphabetically as follows: A = Brownsville, Texas; B = Cuddeback Lake, California; C = Newark, California; and D = Lost River Ranch, Alberta.

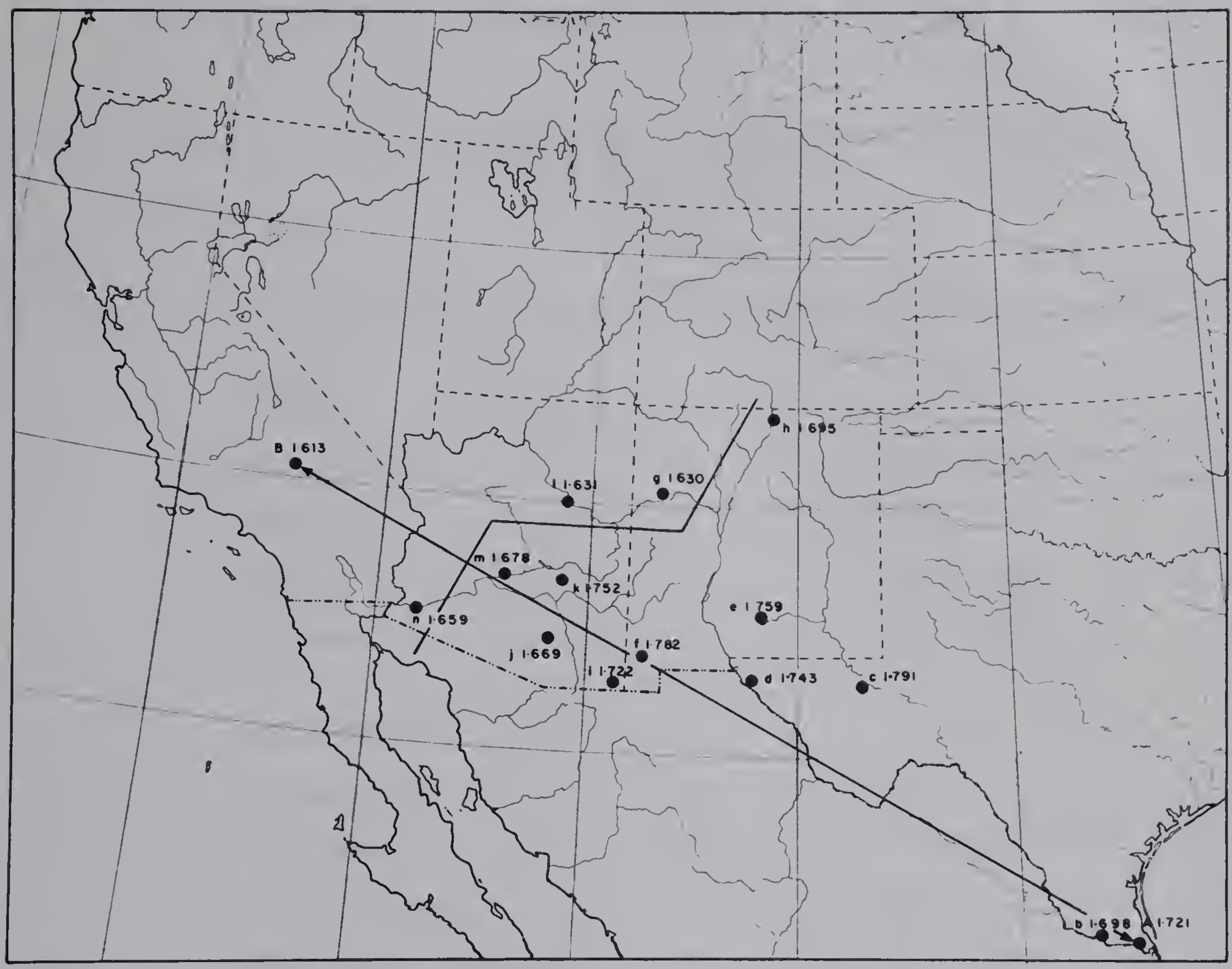


Fig. 2. Plotted mean Z_i values of selected population samples of <u>Tecnophilus croceicollis</u> Menetries used in the comparison of populations from Brownsville, Texas (A) to Cuddeback Lake, California (B). The mid-point Z_i value equals 1.667. Association of letters and locality names are made in Table 12.

Table 12. $\overline{Z}_i$ values calculated for selected population samples of Tecnophilus croceicollis Menetries from the discriminant function developed for the Brownsville, Texas (A) vs Cuddeback Lake, California (B) populations comparison (mid-point $\overline{Z}_i$ value is 1.667)

Map symbol	Locality	Comparison A vs B Number of specimens	Range	$\overline{Z}_i$
	TEXAS			
A	Brownsville	20	1.667-1.799	1.721
b	Mission	1	1.698	1.698
c	Pecos	2	1.782-1.800	1.791
d	Fabens	5	1.726-1.786	1.743
	NEW MEXICO			
e	Alamogordo	1	1.759	1.759
f	Lordsburg	7	1.716-1.886	1.782
g	Fort Wingate	1	1.606	1.606
h	San Juan Valley	2	1.655-1.736	1.695
	Coolidge (?)	5	1.605-1.668	1.630
	ARIZONA			
i	San Bernardino	2	1.718-1.725	1.722
j	Tuscon	1	1.669	1.669
k	Globe	1	1.752	1.752
l	Winslow	5	1.592-1.664	1.631
m	Tempe	1	1.678	1.678
n	Palomas	1	1.617	1.617
o	Welton	5	1.605-1.696	1.659
	CALIFORNIA			
B	Cuddeback Lake	64	1.541-1.701	1.613

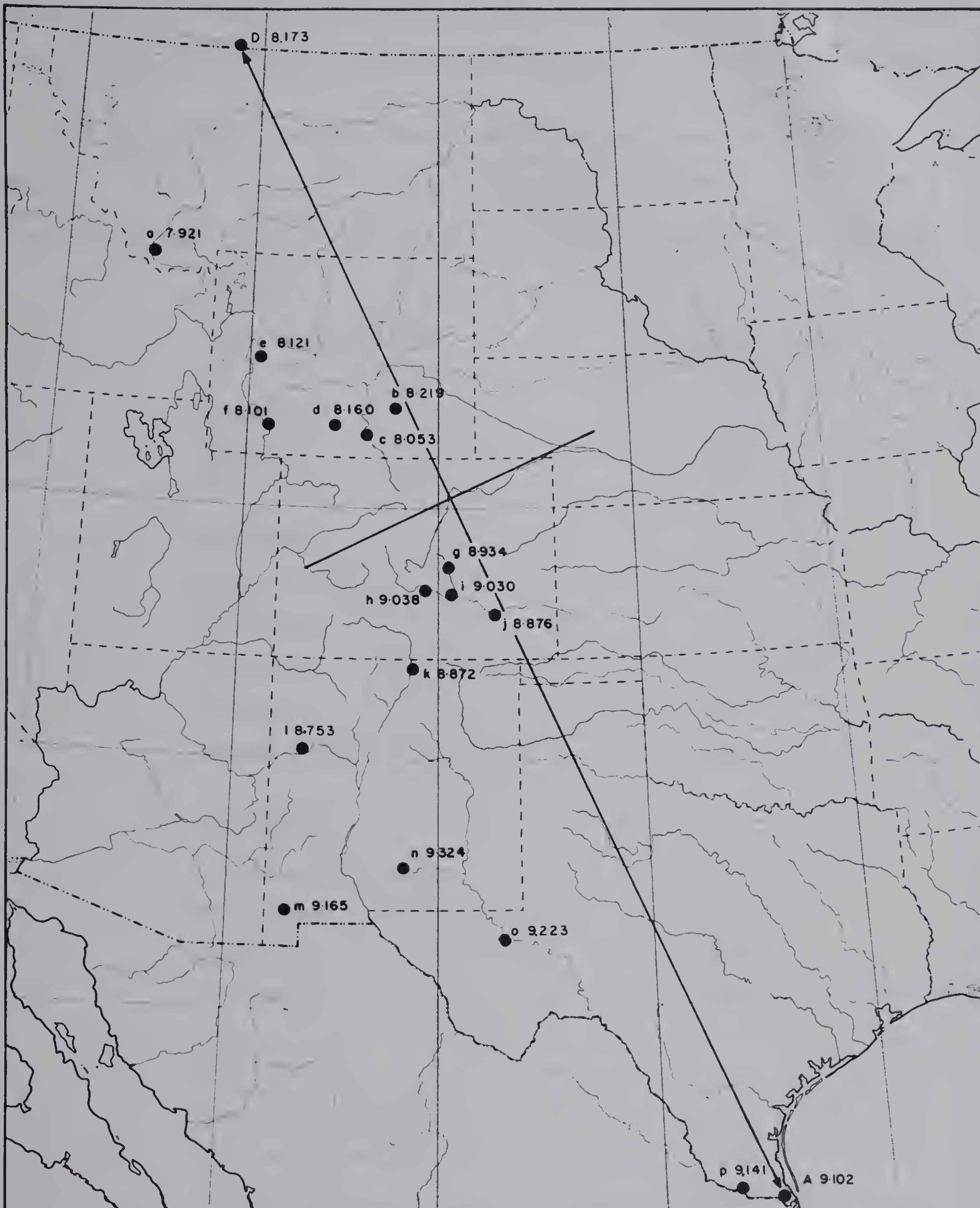


Fig. 3. Plotted mean Z_i values of selected population samples of Tecnophilus croceicollis Menetries used in the comparison of populations from Brownsville, Texas (A) to Lost River Ranch, Alberta (D). The mid-point Z_i value equals 8.596. Association of letters and locality names are made in Table 13.

Table 13. $\overline{Z}_i$ values calculated for selected population samples of Tecnophilus croceicollis Menetries from the discriminant function developed for the Brownsville, Texas (A) vs Lost River Ranch, Alberta (D) populations comparison (mid-point $\overline{Z}_i$ value is 8.596)

Map symbol	Locality	Number of specimens	Range	$\overline{Z}_i$
	ALBERTA			
D	Lost River Ranch	38	7.783-8.379	8.173
	MONTANA			
a	Dillon	1	7.921	7.921
	WYOMING			
b	Medicine Bow	1	8.249	8.249
c	Saratoga	2	7.974-8.133	8.053
d	Creston	2	8.110-8.210	8.160
e	Pinedale	1	8.121	8.121
f	Green River	1	8.101	8.101
	COLORADO			
g	Colorado Springs	2	8.769-9.099	8.934
h	Florence	1	9.038	9.038
i	Pueblo	1	9.030	9.030
j	La Junta	1	8.876	8.876
	NEW MEXICO			
k	San Juan Valley	2	8.618-9.124	8.872
l	Ft. Wingate	1	8.465	8.465
m	Lordsburg	7	9.031-9.457	9.165
n	Alamogordo	1	9.324	9.324
	TEXAS			
o	Reeves Co., Pecos	2	9.150-9.296	9.223
p	Mission	1	9.141	9.141
A	Brownsville	20	8.967-9.291	9.102

northern Colorado. This line is concordant with a change in color and a change in eye shape.

Cuddeback Lake, California versus Newark, California (Comparison B-C).- Calculated $\bar{Z}_i$ values are presented in Table 14 and Fig. 4, in the same way as above. The discriminant function gives poor separation of specimens from the two populations used in the original comparison. It provides even poorer separation of specimens from intermediate localities. Specimens with intermediate $\bar{Z}_i$ values are found in the northern portions of the San Joaquin Valley and this change is not concordant with a change in the state of any other character. Like color, $\bar{Z}_i$ values vary clinally.

Cuddeback Lake, California versus Lost River Ranch, Alberta (Comparison B-D).- Calculated $\bar{Z}_i$ values are presented in Table 15 and Fig. 5 in the manner outlined above. In this case, the transverse line representing the approximate location of specimens possessing mid-point $\bar{Z}_i$ values, is in northern Utah. $\bar{Z}_i$ values for specimens collected from localities in close proximity to this line, tend to intergrade into each other. Color and vestiture also change through this region.

Summary.- Because of lack of concordance in the variation patterns among the characters studied, the population samples A, B and C are considered to be consubspecific. However, several characteristics differentiating population samples A and D change in the same area. Also, several characteristics differentiating population samples B and D change in the same area. I conclude therefore, that population sample D and specimens associated with it are subspecifically distinct from samples A, B and C and their associated specimens.

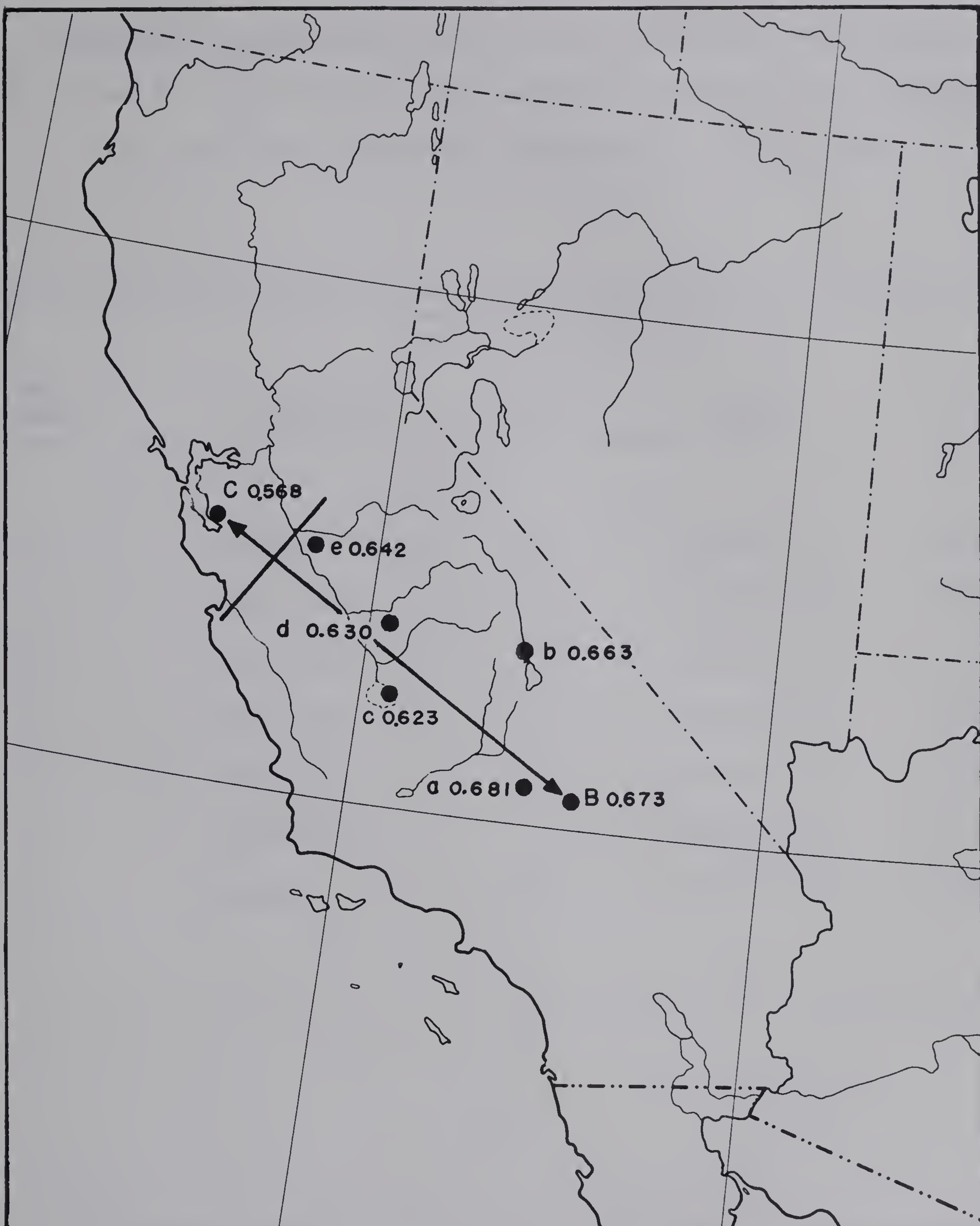


Fig. 4. Plotted mean Z_i values of selected population samples of Tecnophilus croceicollis Menetries used in the comparison of populations from Cuddeback Lake, California (B) to Newark, California (C). The mid-point Z_i value equals 0.621. Association of letters and locality names are made in Table 14.

Table 14. $\overline{Z}_i$ values calculated for selected population samples of *Tecnophilus croceicollis* Menetries from the discriminant function developed for the Cuddeback Lake, California (B) vs Newark, California (C) populations comparison (mid-point $\overline{Z}_i$ value is 0.621)

		Comparison B vs C		
Map symbol	Locality	Number of species	Range	$\overline{Z}_i$
B	Cuddeback Lake	64	0.622-0.773	0.673
a	Koehn Lake	7	0.645-0.780	0.681
b	Lone Pine	3	0.632-0.690	0.663
c	Kings Co.	4	0.594-0.649	0.623
d	Fresno Co.	4	0.605-0.656	0.630
e	Merced Co.	3	0.624-0.653	0.642
C	Newark	40	0.492-0.648	0.568

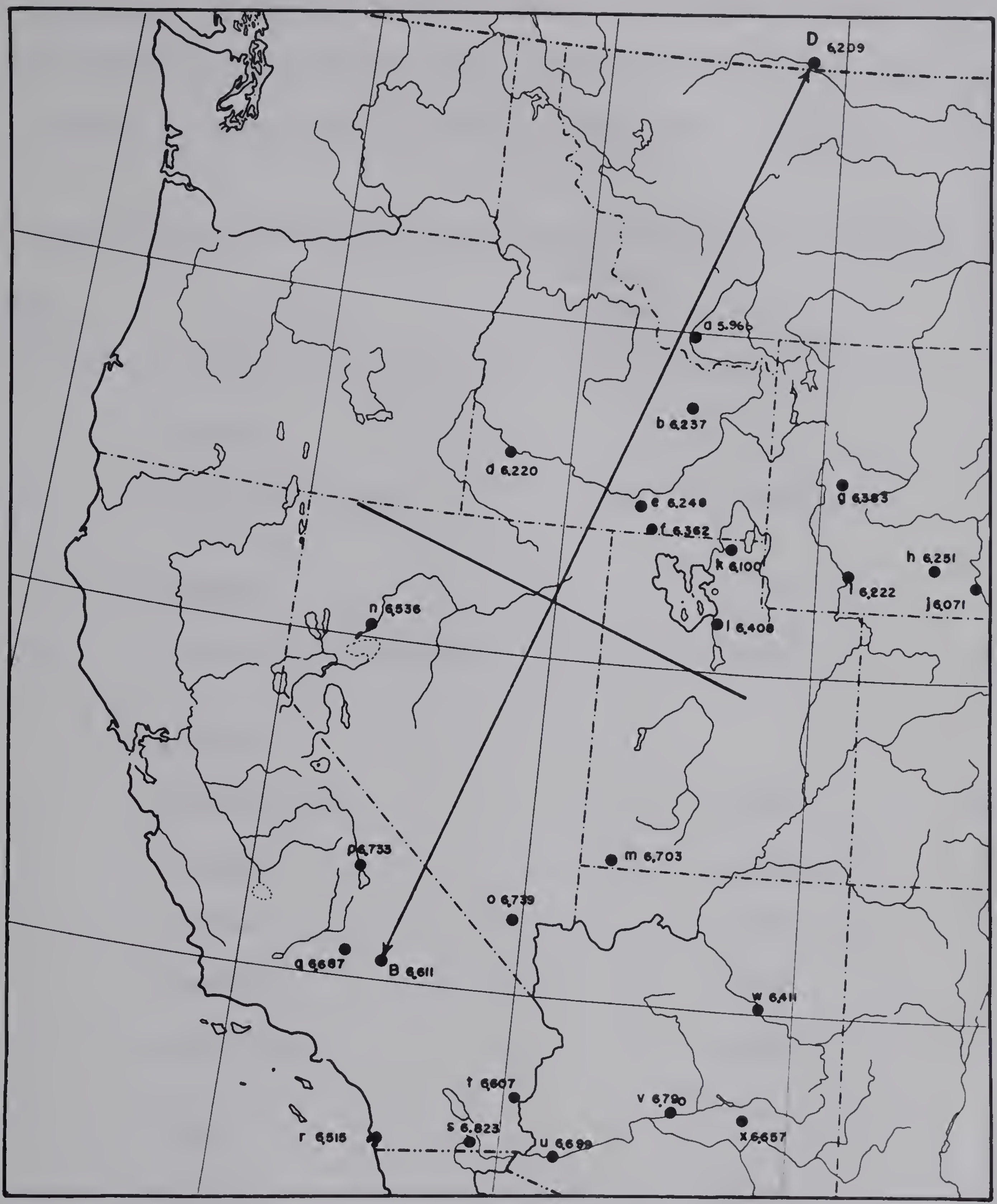


Fig. 5. Plotted mean Z_i values of selected population samples of Tecnophilus croceicollis Menetries used in the comparison of populations from Cuddeback Lake, California (B) to Lost River Ranch, Alberta (D). The mid-point Z_i value equals 6.410. Association of letters and locality names are made in Table 15.

Table 15. $\overline{Z}_i$ values calculated for selected population samples of <u>Tecnophilus</u> <u>croceicollis</u> Menetries from the discriminant function developed for the Cuddeback Lake, California (B) vs Lost River Ranch, Alberta (D) populations comparison (mid-point $\overline{Z}_i$ value is 6.410)

Map symbol	Locality	Number of specimens	Range	$\overline{Z}_i$
	ALBERTA			
D	Lost River Ranch	38	5.926-6.308	6.209
	MONTANA			
b	Dillon, Beaverhead Co.	1	5.966	5.966
	WYOMING			
c	Medicine Bow	1	6.087	6.087
d	Saratoga	2	6.052-6.099	6.071
e	Creston	2	6.235-6.267	6.251
f	Pinedale	1	6.383	6.383
g	Green River	1	6.222	6.222
	IDAHO			
h	Viola	1	5.710	5.710
i	Howe	1	6.237	6.237
j	Strevell	1	6.362	6.362
k	Malta	1	6.248	6.248
l	Grandview	1	6.220	6.220

Table 15 (cont'd)

Map symbol	Locality	Number of specimens	Range	$\bar{Z}_i$
	UTAH			
m	Logan	1	6.100	6.100
n	Salt Lake City	6	6.267-6.488	6.408
o	St. George	5	6.510-6.866	6.703
	NEVADA			
p	Humbolt Lake	2	6.403-6.669	6.536
q	Las Vegas	2	6.651-6.827	6.739
	CALIFORNIA			
r	Lone Pine	3	6.567-7.056	6.733
s	Koehn Lake	7	6.499-6.804	6.687
B	Cuddeback Lake	64	6.421-6.871	6.611
t	San Diego	2	6.494-6.536	6.515
u	El Centro	3	6.690-6.906	6.823
v	Palo Verde	4	6.411-6.719	6.607
	ARIZONA			
w	Welton	5	6.489-6.982	6.699
x	Tempe	3	6.724-6.866	6.790
y	Winslow	5	6.410-6.537	6.411
z	Globe	1	6.657	6.657

Key to the subspecies of _Tecnophilus croceicollis_ Menetries

1\. Specimens from California . . . . . _c. croceicollis_ Menetries p.

1'. Specimens from localities other than California 2

2(1). Color of head, pronotum and legs rufous; eyes large and convex (Fig. 25) . . . . _c. croceicollis_ Men. p. 88

2'. Color not as above; if head, pronotum and legs basically rufous in color, at least tarsi, clypeus and frons between eyes somewhat infuscated: eyes small and flat (Fig. 24) . . . . _c. peigani_ new subspecies p. 91

OR

2a(1). Specimens from west of Rocky Mountains 3

2a'. Specimens from east of Rocky Mountains 4

3(2). $(-3.281)WP/LP + (-0.223)LE + (2.023)WH_1/WH_2 + (1.396)LE/LP + (3.768)WP/WH > 6.410$ . . . . _c. croceicollis_ Men.

3'. "+"+"+"+" < 6.410 . . . . _c. peigani_ n. ssp.

4(2). $(0)WP/LP + (-0.053)LE + (3.643)WH_1/WH_2 + (1.165)LE/LP + (0)WP/WH > 8.596$ . . . . _c. croceicollis_ Men.

4'. "+"+"+"+" < 8.596 . . . . _c. peigani_ n. ssp.

Tecnophilus croceicollis croceicollis Menetries, 1843

Calleida croceicollis Menetries, 1843- 54. TYPE LOCALITY.- California.

Callida chloridipennis Motschoulsky, 1850- 39. (from Horn, 1882).

Philotecnus nigricollis LeConte, 1851- 176. TYPE LOCALITY.- San Jose, California.

Philotecnus ruficollis LeConte, 1851- 176. TYPE LOCALITY.- San Diego, California.

Tecnophilus glabripennis Chaudoir, 1877- 242. TYPE LOCALITY.- Nevada.

Specimens of this subspecies may best be recognized on the basis of the combination of characters presented in the key to subspecies of *croceicollis*.

Description.- Values for ratios and measurements of selected population samples of this subspecies are presented in Tables 6 to 10.

Color varied in specimens from the Central Valley of California; head, pronotum and legs basically rufous with at least some infuscation and in some specimens these parts are black; elytra dark blue or purple. Specimens from remainder of range with head, pronotum and legs uniformly rufous; elytra blue to green.

Microsculpture lightly impressed or obsolete on head and disc of pronotum; varied on elytra from granular to lightly impressed and shiny.

Head with eyes large and convex (Fig. 25). Antenna relatively long and slender.

Pronotum varied in shape (Figs. 39 to 41); not so cordate as in *peigani*.

Elytra varied in shape, short and oval in some specimens to more elongate and parallel sided; striae evidently impressed and distinctly punctate; intervals flat to convex, variably punctate.

Male genitalia as in Fig. 19. Similar to that of *T. pilatei* but with a shorter apex.

Female stylus (Fig. 56) truncate apically, not produced.

Discussion.- The high degree of variation shown by this subspecies has led past authors to describe a number of species, or to regard *croceicollis* as a single highly variable species.

Notes on synonomy.- The name pilatei Chaudoir is not a synonym for croceicollis Menetries as is shown above.

MEXICO

DURANGO: Durango (Emburg, CAS).

SINALOA: El Camaron (Ball, UASM).

UNITED STATES

ARIZONA: Cochise Co., San Bernardino Ranch (Snow, UASM); Gila Co., Globe (USNM); Navajo Co., Winslow (USNM); Pima Co., Tucson (MCZ); Yuma Co., Palomas (CU), Wellton (CU).

CALIFORNIA: Alameda Co., Bay Farm Island (Barr, Dahl, CAS, IUM, MCZ), Newark (Tyson, UASM); Butte Co., Oroville (Kelfer, CAS); Contra Costa Co., Antioch (Rose, CAS), Brentwood (Van Dyke, CAS), Vine Hill (Blaisdell, CAS); Fresno Co., Mendota (MCZ); Imperial Co., El Centro (Hanson, Van Dyke, CAS, CU, WUM); Palo Verde (Barr, IUM); Inyo Co., Lone Pine (Van Dyke, CAS), Panamint Valley (USNM), (Nunenmacher, CNHM); Kern Co., Koehn Lake (Erwin, UASM); Kings Co., (CNHM); Lassen Co., (Nunemacher, CNHM); Merced Co., Los Banos (O'Brien, Van Dyke, CAS, UASM); Orange Co., Seal Beach (Gillogly, CAS); Riverside Co., Coachella (Van Dyke, CAS); San Bernardino Co., Barstow (Hayward, MCZ), Cuddeback Lake (Larson & Sharp, UASM); Needles (Kusche, CAS); Santa Clara Co., Alviso (Erwin, Larson & Sharp, UASM); San Diego Co., San Diego (CAS); San Joaquin Co., Weston (Van Dyke, CAS); San Mateo Co., San Mateo (Nunenmacher, Van Dyke, CAS, CNHM); Solano Co., Benica (Car. M); Sonoma Co., Glen Ellen (Kusche, CAS, CNC); Stanislaus Co., Patterson (Ross, CAS); Yolo Co., Davis (Erwin, Hatch, Car. M, UASM, WUM); Yuba Co., Marysville (Van Dyke, CAS).

COLORADO: Bent Co., La Junta (Hayward, MCZ); El Paso Co., Colorado Springs (Soltau, USNM); Freemont Co., Florence (Soltau, USNM); Pueblo Co., Pueblo (Soltau, USNM).

NEVADA: Churchill Co., Humbolt Lake (Wickham, USNM); Clark Co., Las Vegas (Barr, Johnston, CNC, IUM); Pershing Co., Lovelock (Baker, SJSC).

NEW MEXICO: Hidalgo Co., Lordsburg (Howden, CNC); McKinley Co., Ft. Wingate (Dow, CAS); Otero Co., Alamogordo (Wickham, USNM); Taos Co., San Juan Valley (Bowditch, MCZ).

TEXAS: Cameron Co., Brownsville (many collectors, CNC, INHS, MCZ, UASM, USNM); El Paso Co., Fabens (Howden, CNC); Hidalgo Co., Mission (Gurney, USNM); Reeves Co., Pecos (Johnston, CNC), Pecos River ? (Odenbach, USNM).

UTAH: Washington Co., St. George (AMNH, CAS, MCZ, USNM).

Tecnophilus croceicollis peigani new subspecies

HOLOTYPE.- male, Milk River near junction with Lost River, Lost River Ranch, Alberta (12/V/1965, Getty & Larson, CNC)

ALLOTYPE.- female, same locality (CNC)

Paratypes.- All other specimens from Alberta have been labelled as paratypes (see below for list of localities).

The diagnostic characteristics of this subspecies are presented in the above key, and in the discussion of geographical variation in *T. croceicollis*.

Description.- Values for ratios and measurements of this subspecies are presented in Tables 6 to 10.

Color black, with elytra and in some specimens disc of pronotum with dull metallic blue or blue-green lustre; appendages black or piceous. (see following discussion for variation in color).

Microsculpture lightly impressed or obsolete on head and disc of pronotum; isodiametric and coarse on elytra.

Vestiture very short and sparse on specimens from Alberta. Specimens from more southerly localities moderately setose.

Head broad; eyes small and little convex (Fig. 24). Antenna shorter and stouter than in c. croceicollis.

Pronotum strongly cordate (Fig. 42), lateral margins strongly constricted behind, lateral reflexion narrow.

Elytra short and oval, with greatest width in apical half; striae deeply impressed and evidently punctate; intervals convex, each bearing an irregular row of coarse punctures.

Male genitalia (Fig. 20) and female stylus similar to c. croceicollis.

Variation.- Vestiture and color vary over the range of this subspecies. Specimens from the eastern side of the Rocky Mountains are black or at least dark piceous in the color of the head and pronotum. Specimens with this coloration have also been seen from eastern Idaho and extreme northern Utah. However, specimens from central and western Idaho and the Salt Lake region of Utah are much paler in color. In specimens from these regions, the ground color of the head, pronotum and legs is usually rufous, with at least some infuscation occurring on the legs, clypeus and the frons between the eyes. This tendency towards pale coloration in specimens of peigani from Idaho and Utah is probably a result of hybridization with c. croceicollis.

Specimens of peigani from Alberta appear to be almost glabrous dorsally because of the greatly reduced length of the setae. Over the remainder of the range, the dorsal pubescence is longer and quite distinct.

Etymology.- The subspecific name is the latinized form of the word Peigan, the name of a tribe of Indians of the Blackfoot Confederation, which inhabited the prairies of southern Alberta. Confusion exists as to the correct spelling of this name, but the Edmonton office of the Canadian Government Department of Indian Affairs told me "Peigan" was the correct spelling.

Disposition of type material.- The holotype and allotype have been deposited in the Canadian National Collection, Ottawa. Paratypes have been deposited in California Academy of Sciences, Canadian National Collection, Museum of Comparative Zoology, University of Alberta, Strickland Museum, and the United States National Museum.

Distribution.- Localities from which specimens of peigani have been collected are plotted in Fig. 63. I have seen 73 specimens of this subspecies from the following localities.

CANADA

ALBERTA: Forty Mile Coulee, 5 miles north Etzikom (Getty, Larson, Whitehead, UASM); Milk River near junction with Lost River, Lost River Ranch (Ball, Erwin, Freitag, Getty, Larson, CAS, CNC, MCZ, UASM, USNM); Picture Butte (Getty & Larson, UASM).

UNITED STATES

COLORADO: "Col." (USNM).

IDAHO: Butte Co., Howe (Barr, IUM); Cassia Co., Malta (Henry, IUM); Strevell (Barr, IUM); Owyhee Co., Grandview (Furniss, IUM).

MONTANA: Beaverhead Co., Dillon (Jellison, MUB).

UTAH: Cache Co., Logan (Henderson, CAS); Davis Co., (Stafford, USNM); Salt Lake Co., Salt Lake City (J.B., Henderson, Huelleman, Klages, Car. M, IUM, WUM).

WYOMING: Carbon Co., Medicine Bow (AMNH), Saratoga (Bryant, CAS); Sublette Co., Pinedale (Alexander, MCZ); Sweetwater Co., Creston (Bryant, CAS), Green River (Bowditch, MCZ).

6. BIOLOGY

Although little is known of the biology of beetles of the subtribe Callidina, members of many of the species and genera appear to be at least partly arboreal. Habu (1960, 1967) summarized what is known of the biology of members of the genus Callida. Generally, these insects are arboreal predators, feeding mostly on lepidopterous larvae. These insects do not show any of the parasitic adaptations possessed by the members of the genus Lebia.

What I have observed of the biology of the genera Tecnophilus and Philophuga is presented below.

6.1. Biology of Tecnophilus Chaudoir

The biology of these insects is poorly known. Adults of this genus tend to be more terrestrial than are adults of any of the other North American callidine genera. This is reflected in the slender legs and tarsi, setose body and the cordate prothorax of Tecnophilus; characters which are often found in terrestrial carabids, but seldom found in arboreal forms.

Adults are found on saline or alkaline soils in eroding areas. Table 16 presents some of the physical characteristics of the top six inches of the soils on which these insects have been collected. The high soil salinity and the arid conditions in regions in which members of the genus Tecnophilus occur, suggests that desiccation may be an important factor with which these insects must contend. During relaxation of specimens prior to dissection, I noticed that the dried tissues were quite impermeable to water. Immersion in near-boiling water for periods of fifteen minutes to half an hour was not sufficient to soften the abdominal

Table 16. Some physical characteristics of soils on which specimens of *Tecnophilus croceicollis* Menetries have been collected

Locality	Number of soil samples	pH	Electrical conductivity	$CaCO_3$	Na	Cl	Texture
Lost River, Alberta	5	8.1-8.4	0.9-6.0	high	high	trace	packed clay-sand
Alviso, California	2	4.0-4.4	16+	-	extremely high	200+	friable sand
Cuddeback Lake, California	1	7.5	15.0	high	extremely high	200+	sand
Rockport, Texas	1	8.1	8.0	-	very high	180	friable sand

membranes enough to permit the genitalia to be withdrawn easily. This is a longer time than is required to relax most species of Carabids. This impermeability may be an adaptation to resist desiccation under arid conditions.

In southeastern Alberta, specimens of Tecnophilus croceicollis peigani are usually found along the bases of south facing coulees, where considerable erosion has occurred and alluvial fans have been deposited. These fans are composed of a clay-sand soil which bakes and cracks extensively when dry. The sparse vegetation consists principally of Bouteloua gracilis (Lag.) H.B.K., Atriplex nuttalli Wats., Opuntia spp., Mamillaria vivipara Haw., and Erigonum flavum Nutt. A more complete description of the region is presented by Lewin (1963).

On sunny days in May and early June, specimens of c. peigani were found running over the surface of the ground, or climbing on very low vegetation. Infrequently specimens have been taken under cover or from cracks in the ground. At this time, the insects are often found in copulation, and mating occurs readily among captured specimens. Fertile females collected at this time and brought into the laboratory, usually laid eggs within a week or two. Larvae emerging from these eggs were reared as far as the third instar on the following foods: larvae of several species of curculionids, wheat stem sawfly larvae, wax moths, meal worms, and ant larvae and pupae. Mortality was high on all of these foods.

This subspecies probably hibernates in the adult stage, for one specimen from Green River, Wyoming (20-27/VII/1877), was teneral, indicating that emergence from the pupal stage occurs during the middle of the summer. All specimens are fully winged but flight has not been observed.

The habitats in which specimens of _c. croceicollis_ were found, vary over the wide range of this subspecies. The most consistent features of the habitats are saline eroding soils and sparse vegetation.

In the vicinity of San Francisco Bay, beetles have been collected on salt flats, usually in areas dominated by plants of the genus _Salicornia_. During the winter months, these insects are found near or at the surface of the soil, under the _Salicornia_ mats or other loose cover (Erwin, Pers. Com.). However, on July 5, 1966, (Alviso, California, Larson & Sharp collectors) seven specimens were collected at depths of four to eight inches in the sandy soil beneath _Salicornia_ plants. The beetles were on the upper surface of the clay hardpan, and in company with specimens of _Amara stupida_ LeConte and _Pristonychus complanatus_ Dejean. The two teneral specimens that I have seen from the central Valley of California (Marysville, Yuba Co., VI/1908; and Mendota, Fresno Co., V-VIII) suggest that the larval stage occurs during the spring and summer in this region.

Specimens of _c. croceicollis_ have been collected from the margins of several alkaline playas in the Mojave Desert of southeastern California. A long series of beetles collected at Cuddeback Lake (June 30, 1966, Larson & Sharp) was found among the buried portions of the crowns of bur sage (_Franeria dumosa_ Grey) at depths of three to ten inches. Specimens collected at the neighboring Koehn Lake in the spring (April 10, 1965, Erwin) were found at the surface of the soil, under loose cover. I have seen teneral specimens from Lone Pine, California (20/V/1937). The larval stage probably occurs in the early spring as this is the season of greatest rainfall in the Mojave Desert.

All long series of _c. croceicollis_ that I have seen from Texas, have been collected at light. I do not know the habitat of this insect in

Texas, but it appears to occur only in inland localities and not along the Gulf Coast. On the other hand, T. pilatei is found primarily along the coast and only for a short distance inland. A mixed series of both of these species was colected at light in Brownsville, Texas (May, 1967).

Outside of Texas, I have seen only one specimen of croceicollis (s.e. California) labelled as being collected at light.

Most specimens of the species pilatei have been collected at light. However, some at least have been collected by sweeping vegetation along sea beaches (Port Isabel, Ball).

In order to obtain the larvae of Tecnophilus,I maintained adults of c. croceicollis and c. peigani alive. The method of oviposition was observed, and was found to proceed as follows for both subspecies: when ready to lay an egg, the female collected a small ball of soil particles on the apex of her abdomen. These particles were first loosened with the mandibles then picked up singly with the apex of the abdomen to which they adhered, probably by means of an adhesive substance produced by the accessory glands. When sufficient material was collected, the female climbed some object such as a twig. When she had climbed to a height of several inches, the beetle turned and faced downward. The abdomen was pressed against the twig, and a drop of fluid was released. The abdomen was then moved away from the twig, drawing the drop of fluid out until it hardened into a silk-like strand. This strand was formed partly by the movement of the adbomen, and partly by means of an apposable motion of the styli. When the thread reached a length of about 1 to 6 mm, the female injected an egg into the ball of soil particles that she still carried on the apex of her abdomen. The egg and soil covering were then released, and were left dangling in the air, suspended from the twig by

means of the silken thread. The egg remained suspended in this way until the larva hatched.

This method of oviposition may be related to the peculiar form of stylus that is found in members of the Callidina. Philophuga viridis amoena, which possesses a similar form of ovipositor, lays its eggs in the same way. This form of egg laying could certainly be a valuable adaptation for desert species, for it would protect the eggs to some extent from most predators, flash floods, and soil erosion. On the other hand, it would make the eggs more susceptible to desiccation. As the rest of the members of the Callidina possess this form of ovipositor, and are more or less arboreal, this form of egg laying was probably an adaptation to an arboreal existence, and has secondarily proved useful to desert dwelling species.

6.2. Biology of Philophuga Motschoulsky

As I have collected few specimens of the genus Philophuga, I know little of the habits of these insects. In general, members of this genus occur in arid and semi-arid regions of western North America. They are not usually found in saline situations as are members of the genus Tecnophilus, and they appear to be much more arboreal than the latter, for specimens of Philophuga are often found on vegetation.

In southern Alberta, specimens of P. viridis amoena are found in the same general region as are specimens of T. croceicollis peigani. However, rather than occurring along the bases of coulees in regions of baked soil and sparse vegetation, they are usually found on short grass prairie.

Many of the specimens of P. viridis horni that I have examined, are associated with labels indicating that they have been collected on

vegetation, usually _Artemisia_ or _Atriplex_. I know nothing of the biology of the other subspecies of _viridis_ except that most specimens of _v. viridis_ that I have examined were collected during the month of December.

The labels associated with many adult specimens of _P. viridicollis_ indicate that the beetles were collected on vegetation. Four specimens of this species collected at Monahans, Texas (Larson & Sharp, June 12, 1966) were found on a short legume, in leaf rolls made by a lepidopterous larva. Larvae of _viridicollis_ have been collected at Rocky Ford, Colorado (Hamilton, USNM. See section 4.4.3.) feeding on the larvae of _Ancylis comptana_ W. & R. (Lepidoptera: Olethreutidae). Teneral adults of this species have been collected from April 28 to July 5.

Specimens of _P. brachinoides_ have been collected in bromeliads (Ball & Whitehead, see section 5.2.2.).

I have not seen any records of specimens of the genus _Philophuga_ collected at light.

In this genus, oviposition has been observed only for the subspecies _viridis amoena_. It proceeds in the same way as outlined under _Tecnophilus croceicollis_.

7. PHYLOGENY

The following discussion is an explanation of the rationale used to construct the phylogenetic diagram presented in Table 17. In order to construct this model, two assumptions had to be made: (a) it is possible to discover those characteristics that are widespread in the group due to common ancestry, and to distinguish these from similar characteristics that have resulted from convergence (Cain and Harrison, 1960); and (b) the rate of evolution has been uniform throughout the group, so that the degree of difference between two taxa is directly proportional to the length of time for which the two ancestral stocks have been isolated. These assumptions are necessitated by the complete lack of fossil evidence.

Based on these considerations, the following hypothetical model of the evolution of the North American Callidina is presented. The ancestral stock was probably arboreal, and possessed the following characteristics: color of elytra metallic blue or green, color of remainder of body rufous to black; dorsal surface of body glabrous; labial palpus with terminal article securiform, penultimate article bisetose; ligula bi- or plurisetose; prothorax broad, with wide lateral reflexion; legs stout, with tarsal article 4 bilobed, claws pectinate, ventral surface of tarsal articles 1 to 4 of front and middle tarsi of male bearing two rows of scales beneath; elytra completely bordered basally and apically, striae evident and punctate, intervals flat or slightly convex; hind wings fully developed and lightly pigmented; abdominal sterna 4, 5, and 6 lacking lateral setae, sternum 6 with a small number of anal setae (probably three pairs or less); male genitalia on their right side in repose, with

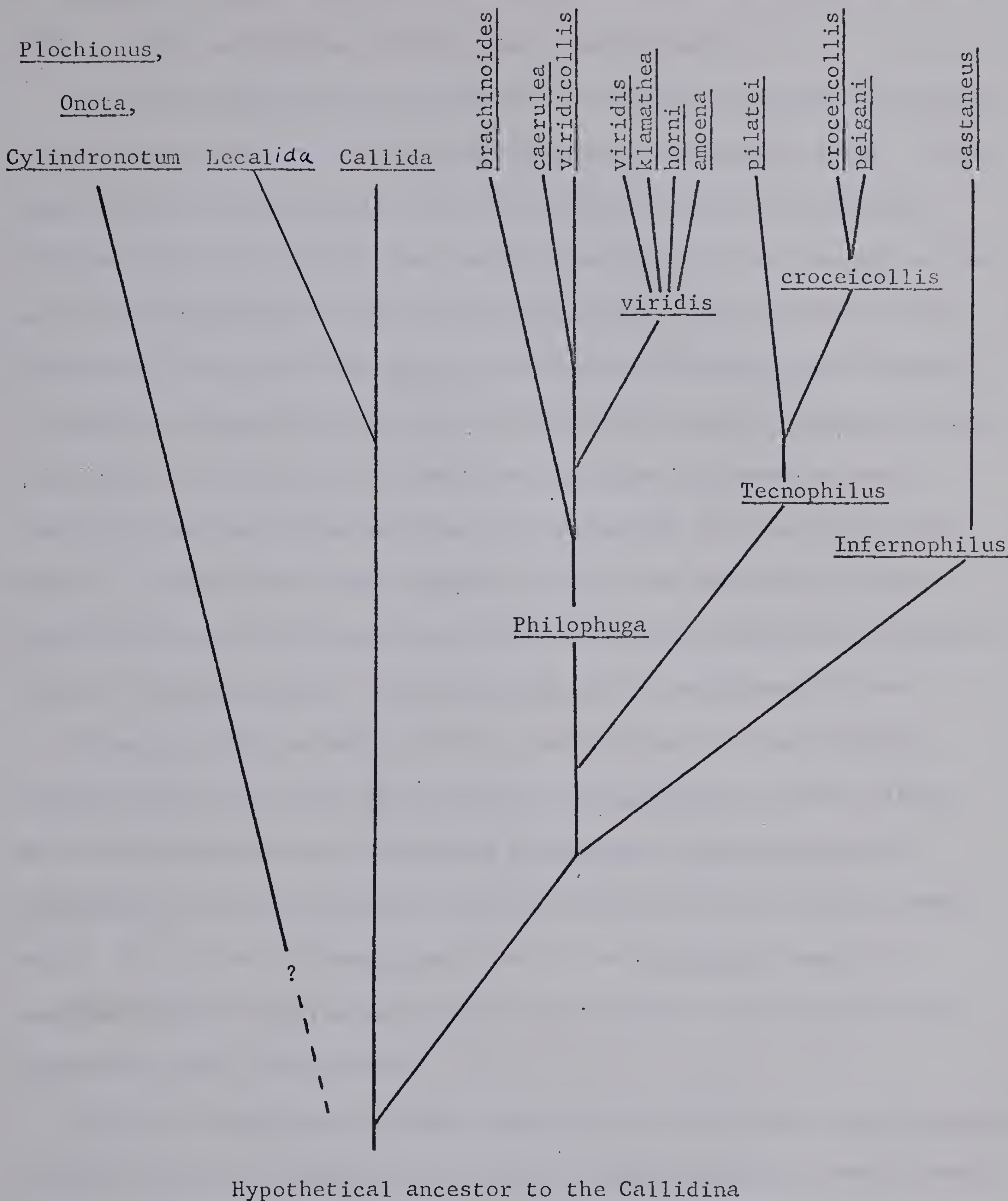


Table 17. Hypothetical phylogeny of the endemic North American genera of the subtribe Callidina and their included species.

left paramere large; endophallus armed or unarmed; female stylus rectangular, lightly sclerotized, with a setose apical margin.

An early differentiation of the basic callidine stock may have given rise to the ancestor of the Plochionus-Onota-Cylindronotum lineage. This group differs in many details from the remaining members of the North American Callidina, and has been included in the Callidina largely on the basis of the structure of the female ovipositor. The structure of the ovipositor as well as other external features of this group may resemble the condition found in the hypothetical callidine ancestor simply through convergence. If this is the case, the Callidina represents a grade, resulting from parallel adaptation to a common way of life, an arboreal habitat. As mentioned above (section 4.4.1.), the affinities of this group are obscure and probably are among the poorly understood neotropical fauna. For this reason, this group will not be considered further.

A later differentiation of the ancestral stock of the Callidina probably gave rise to the genera Callida and Lecalida with very little additional modification. The genera Philophuga, Infernophilus and Tecnophilus are closely related, and were probably derived from a common stock. This stock differentiated from the main Callida lineage by aquiring slender legs (tarsal article 4 not bilobed, but only shallowly emarginate) and a setose body.

The most distinctive of these three genera, is the genus Infernophilus. For this reason, the ancestor to the genus Infernophilus may have diverged from the Philophuga-Tecnophilus stock early in its history, in order to permit the Infernophilus stock sufficient time to acquire the characteristics listed below. This genus exhibits a peculiar form of male genitalia which has undergone 180° rotation. The mechanism which brought this

reversal about is unknown, but it seems reasonable to postulate that the initial change involved a 180° shift in the orientation of the aedeagus. The reversal of the parameres may have accompanied this initial reversal of the aedeagus or they may have rotated at a later date. In this genus, other peculiar characters include the anal brushes, the non-metallic elytra, and the short, rounded female styli.

The stocks giving rise to Philophuga and Tecnophilus separated sometime after the separation of the Infernophilus stock. The stock giving rise to the genus Philophuga remained essentially unmodified after this point, but the stock ancestral to Tecnophilus acquired simple tarsal claws, a more cordate pronotum, and a more densely setose body.

The stock giving rise to the genus Philophuga probably possessed the following characters, as these are the most wide-spread characteristics in species of this genus: color of entire body except for basal antennal articles, black with a metallic blue or green lustre dorsally; body sparsely setose; pronotum sub-cordate, bearing posterior-lateral seta on each hind angle; elytra elongate and more or less parallel sided, with greatest width in apical half; hind wings fully developed, lightly pigmented.

An early derivative of this stock gave rise to the ancestor to the viridis complex. This stock was characterized by shorter, more oval shaped elytra and by a more cordate pronotum. The stock giving rise to viridis has undergone considerable recent diversification to give rise to the four extant subspecies. These four subspecies may have developed simultaneously from four isolated populations, as no subspecies is strikingly distinct.

The other ancestral stock of the genus Philophuga gave rise to the extant species viridicollis, caerulea and brachinoides. The ancestor to these species possessed deeply pigmented wings and elongate elytra. This stock gave rise first to the uniquely colored species brachinoides which also differs from the other two species in this group by having a more cordate pronotum, and also possesses several patches of setae on the ventral surface of the body. The two extant species caerulea and viridicollis are the result of relatively recent diversification in the ancestral stock.

The ancestral stock of the genus Tecnophilus may have divided early in its history to give rise to the species pilatei and croceicollis. Recent differentiation has produced two subspecies and a great deal of geographical variation in the species croceicollis.

8. ZOOGEOGRAPHY

The subtribe Callidina is represented in all major zoogeographical regions of the world. However, the greatest diversity in both numbers of genera and species occurs in tropical and subtropical areas. Only two genera contain members in both the Old and New Worlds. The majority of the species included in the genus Plochionus are restricted to the New World, but the species Plochionus pallens Fabricus has been widely distributed by commerce, and is now almost cosmopolitan. Only the genus Callida is represented naturally in Asia, the Americas and perhaps Africa (but see Jeannel, 1949).

At present, the range of the genus Callida is disjunct. The majority of the American species occur in the tropics, but some species in Eastern North America extend north into the southern portion of the cold temperate region. No members of the genus Callida occur in Western North America, hence the New World species of Callida are separated from the oriental members of this genus by a wide geographical gap of apparently unsuitable habitat.

In Western North America, the genera Lecalida, Philophuga, Infernophilus and Tecnophilus, replace the genus Callida.

Many of the morphological and biological adaptations shown by members of the subtribe Callidina, are adaptations for an arboreal existence. It then seems reasonable to assume that present and past distributions of these insects have paralleled the distributions of floral types that have provided suitable habitats.

While no fossil record is available for this group of carabids, adequate fossils have been discovered to enable us to extrapolate the

movements of Tertiary floras in North America. Thus, it is necessary to review the events influencing floral dispersal in Western North America during the Tertiary and Pleistocene in order to reconstruct the history of the callidine genera which are endemic to this region.

The following review is based largely on a paper by Axelrod (1959). Other papers from which this brief review is drawn are: Axelrod 1948, 1950, 1957, 1958; Blackwelder 1948, 1954; Cohn 1965; Dillon 1956; King 1958; MacGinitie 1958, and Martin 1958.

During the early Cenozoic, three geofloras were found in Western North America. The southern portion of the continent was occupied by the broad-leaved evergreen Neotropical-Tertiary Geoflora, while the northern and central portions were covered by the temperate Arcto-Tertiary Geoflora of mixed deciduous hardwoods and conifers. Between them, in Central Southwestern North America, small areas of semi-arid vegetation of the Madro-Tertiary Geoflora were making their initial appearances.

The Eocene environment was one of low relief and low altitude, and the climate was warm and humid. These conditions permitted widespread distribution and migration of plants, and during this time, the Neotropical-Tertiary Geoflora moved northward along the Pacific coast into Alaska, and to or near the Canadian border interiorly. This Geoflora was dominated by broad-leaved evergreens of tropical families and genera which now find their closest counterparts in subtropical forests such as those presently found from southern Mexico to Panama, and in Southern Asia, where annual rainfall is high and the climate is uniformly warm. The Coast Ranges and the eastern Cordilleras did not exist at this time, and the desert flora that now occupies the intervening region was not then in existence.

The cooler, drier climate following the Eocene gradually restricted the Neotropical-Tertiary Geoflora southward, and coastward where it persisted in warm coastal valleys of California and Oregon until into the Miocene, with a few relicts surviving into Pleistocene times. No plants in the United States today represent direct descendants from this flora. However, some genera and species were secondarily derived from it. These derivatives represent subtropic to warm temperate groups that become adapted to the expanding dry subtropical and warm temperate areas of Southwestern North America.

During the early Tertiary, the Arcto-Tertiary Geoflora had a holarctic distribution at high and middle latitudes, and probably was continuous across the Bering Land Bridge that was present during early Eocene times. In Western North America, three principal elements comprised this Geoflora: the Western American element consisting of fossil species related to present day dominants of the coastal and mountain forests; the Eastern North American element consisting of deciduous hardwoods related to those of present Eastern North America; and the East Asian element consisting of mixed deciduous forest species which are no longer native to North America, or have a discontinuous distribution in Eastern North America and Eastern Asia.

Species of these three elements were mixed in a forest of a rather generalized floristic composition. However, the Geoflora was not homogenous throughout its area. It was composed of several forest types, depending upon geographical occurrence and climatic conditions. In response to gradual development of increasingly more emergent continents following early Tertiary, and to the accompanying trend toward lower temperature, this Geoflora gradually migrated southward from near the

Canadian border where it occurred in the early Eocene, to central Nevada and northern California by the middle Oligocene. During the Miocene and early Pliocene, the increasing aridity further restricted this flora to more humid coastal and upland sites. Species belonging to the Eastern American and Eastern Asian elements were rapidly reduced in Western North America during the late Tertiary due to the reduction in summer rains brought about by uplifts in the Coast Ranges and Sierra Nevadas. Only a few of these forms lingered on into the late Pliocene in the mild coastal strip from central California north, becoming extinct here in the early part of the Pleistocene.

The species now dominating the western coniferous forests represent the surviving western American element of the old Arcto-Tertiary Geoflora. In the west, its species became adapted to a climate which was typified by winter rain and summer drought. Its major communities were differentiated chiefly in the latter Pliocene when important topographical changes such as the rise of the Sierra Nevada and the Coast Ranges produced more diverse climates.

The Madro-Tertiary Geoflora which originated in Southwestern North America, was comprised of small-leaved, drought-deciduous, sclerophyllous plants. These plants were derived primarily from the Neotropical-Tertiary Geoflora and to a lesser extent from the Arcto-Tertiary Geoflora in response to the expanding dry climate. Fossil plants, apparently ancestral to Madro-Tertiary species have been discovered in late Cretaceous and Paleocene floras of Southwestern North America. This Geoflora had come into existence by the middle Eocene, and spread over the southwestern part of the continent during succeeding epochs as dry climates expanded. Part of the desert flora as well has been derived from this Geoflora.

In the middle Pliocene, the rapid expansion of dry climates almost completely eliminated woodland and chaparral from the lowlands of the present desert regions. In the later Pliocene and Pleistocene, the rapidly rising Cascades, Sierra Nevada and more easterly mountain ranges brought a drier climate to their lee, and a desert flora came into existence. Its species were derived from those represented in the Geofloras that dominated the area earlier in the Pliocene. The colder Great Basin received increments from the surviving Arcto-Tertiary Geoflora; the Sonoran and Mojave Deserts from the Madro-Tertiary Geoflora.

Considering the present distribution of the genus Callida, it seems that the coniferous forests, semi-arid regions and colder climates of Northern and Western North America provide unsuitable habitats for the species of this genus, and effectively isolate the few Asian species of Callida from the diverse American fauna. This distribution suggests that a faunal connection between Asia and North America occurred in the past.

The Bering Land Bridge which existed during Eocene times was probably forested by elements of the Arcto-Tertiary Geoflora, which at this time had a holarctic distribution at high latitudes. This would provide a pathway through which the ancestors of the Oriental species of Callida could disperse from the New World. At this time, the ancestral stock of Callida was probably trans-continental in North America. Following the Eocene, cooler climates restricted the Arcto-Tertiary Geoflora southward, away from the Bering region, permanently isolating the American and Asian callidine faunas. The latest at which this separation could have occurred would have been the Oligocene or the early Miocene. During the Miocene and Pliocene epochs, increasing aridity in Western North America

gradually eliminated much of the deciduous element of the Arcto-Tertiary Geoflora from this region, and with this sector of the flora, the ancestral species of Callida were restricted to the eastern and southern portions of the continent.

With the expansion of dry climates and the Madro-Tertiary Geoflora during the late Tertiary, a stock of the ancestral Callida developed adaptations for a more terrestrial existence, and occupied the semi-arid and arid regions of the west.

The descendants of this stock, Philophuga, Tecnophilus, and Infernophilus, more closely resemble eastern North American species of Callida than they do Mexican species. Hence, they were probably derived from the Arcto-Tertiary fauna, rather than from a Neotropical-Tertiary ancestor. On the other hand, the genus Lecalida resembles many of the Mexican species of Callida, and may be a northern extension of this group into the North American deserts. Thus, it is probably derived from a Neotropical-Tertiary ancestor.

The time and place of origin of the genus Infernophilus are obscure, for I know nothing of the habits of this genus and hence cannot trace the development of the necessary habitat.

After acquiring the basic terrestrial adaptation of slender legs, the ancestral stock of Philophuga has persisted with little modification. The derivative stock giving rise to Tecnophilus has acquired a number of specializations. This stock was derived from the stock ancestral to Philophuga probably during the Pliocene, as increased aridity resulted in the production of suitable habitats in the form of large salt flats and alkaline playas.

During the early Pliocene, the environment of Western North America was one of low relief, and extensive plains covered much of this region. Mountains were not effective barriers at this time. During this period, the ancestral stock of Philophuga may have ranged widely throughout this area. Crustal unrest and the renewed mountain building processes of the later Pliocene probably isolated populations that evolved into the ancestors of brachinoides, viridis and caerulea-viridicollis.

The subspecies of viridis and the species caerulea and viridiocollis do not appear to be completely separated from one another at present by geographical barriers such as mountains. The isolations that led to the evolution of these groups probably developed during glacial periods of the Pleistocene when mountain glaciers separated populations in the northern deserts and increased rain fall resulted in expanding forests which produced ecological barriers in the southern deserts.

At this time, the same factors isolated populations of Tecnophilus croceicollis, and produced the geographical variation now shown by this species. I do not know what factors led to the isolation of croceicollis and pilatei. Perhaps pilatei was isolated on the Gulf Coast of Texas, and the presence of croceicollis in Texas is the result of a recent invasion from the west.

Floral movements have profoundly influenced the distribution and evolution of the Callidina. Thus, the endemic callidine fauna now found in Western North America is the result of climatic, geological and resulting floral changes which have occurred in this region in Tertiary times.

9. REFERENCES

Axelrod, D. I. 1948. Climate and evolution in Western North America during middle Pliocene time. Evolution 2: 127-144.

_____ 1950. Evolution of desert vegetation in Western North America. Publ. Carneg. Instn. 590: 215-306.

_____ 1957. Late Tertiary floras and the Sierra Nevadan uplift. Bull. geol. Soc. Amer 68: 19-46.

_____ 1958. Evolution of the Madro-Tertiary Geoflora. Bot. Rev. 24: 433-509.

_____ 1959. Geological history. In Munz and Peck, A California flora. University of California Press, Los Angeles, Calif. 1681 p.

Ball, G. E. 1963. Carabidae, Fascicle 4. In Arnett, R. H. The beetles of the United States (A manual for identification). The Catholic University of America Press, Washington, D. C. pp. 55-210, 58 figs.

_____ 1966. A revision of the North American species of the subgenus *Cryobius* Chaudoir (*Pterostichus*, Carabidae, Coleoptera). Opusc. ent., Suppl. 28, 166 p.

Bates, H. W. 1883. Biologia Centrali-Americana, Insecta, Coleoptera, Carabidae, Cicindelidae suppl., vol. 1, pt. 1, p. 153-256, pls. vi-xii.

Blackwelder, E. 1948. The Great Basin. 1. The geological background. Bull. Univ. Utah geol. Ser. 38(20), 16 p.

_____ 1954. Pleistocene lakes and drainage in the Mojave region of southern California. Bull. Calif. Min. Bur. 170: 35-40.

Blackwelder, R. E. 1944. Checklist of the Coleopterous insects of Mexico, Central America, the West Indies, and South America. Part 1. U.S. Natl. Mus. Bull. 185, 188 pp.

Bigelow, R.S., and C. Reimer. 1954. An application of the linear discriminant function to insect taxonomy. Can. Ent. 86(2): 69-73.

Cain, A. J., and G. A. Harrison. 1960. Phyletic weighting. Proc. zool. Soc. Lond. 135: 1-31.

Casey, T. L. 1913. Studies in the Cicindelidae and Carabidae of America. In Casey T. L. Memoirs on the Coleoptera. IV. New Era Printing Company, Lancaster, Pa. 192 p.

_____ 1924. Additions to the known Coleoptera of North America. In Casey, T. L., Memoirs on the Coleoptera. XI. New Era Printing Company, Lancaster, Pa. 347 p.

Chaudoir, M. de. 1842. Description de quelques genres nouveaux de la famille des carabiques. Bull. Soc. Imp. Nat. Moscou. 15: 832-857.

_____ 1872. Monographie des callidides. Ann. Soc. ent. Belg. 15: 97-204.

_____ 1877. Genres nouveaux et espèces inédites de la famille des carabiques. Bull. Soc. Imp. Nat. Moscou 52: 188-268.

Chevrolat, L. A. A. 1835. Coléoptères du Mexique, fasc. 5. Strasbourg 50 p.

Cohn, T. J. 1965. The arid-land katydids of the North American genus <u>Neobarrettia</u> (Orthoptera: Tettigoniidae): Their systematics and a reconstruction of their history. Misc. Publ. Mus. Zool. Univ. Mich. 126, 179 p.

Csiki, E., 1932. Harpalinae VII. In Junk, W., and S. Schenkling (editors). Coleopterorum Catalogus. 11. Berlin and s' Gravenhage. p. 1279-1598.

Dejean, P. F. M. A. 1831. Species général des coléoptères de la collection de M. le compte Dejean. Vol. V. 883 p. Paris.

Dillion, L. S. 1956. Wisconsin climate and life zones in North America. Science 123: 167-176.

Emden, F. Van. 1942. A key to the genera of larval Carabidae. Trans. R. ent. Soc. Lond., 92: 1-99, 100 figs.

Freitag, R. 1965. A revision of the North American species of the Cicindela maritima group with a study of hybridization between Cicindela duodecimguttata and oregona. Quaest. ent. 1(3): 87-170.

Goulden, C.H. 1952. Methods of statistical analysis. J. Wiley & Sons, Inc., New York. 467 p.

Habu, A. 1960. Callida-species of Japan (Coleoptera, Carabidae). Bull. Nat. Inst. Agr. Sci., (C) 12: 155-169.

_____ 1967. Fauna Japonica: Carabidae Truncatipennes group (Insecta: Coleoptera). Tokyo Electrical Engineering College Press Tokyo. 338 p., XXVII pls.

Hatch, M. H. 1950. An account of the life of Orson Bennett Johnson, p. 11-28. In Studies honoring Trevor Kincaid.

_____ 1953. The beetles of the Pacific northwest. Univ. Wash. Publ. Biol. 16, 340 p.

Horn, G. H. 1881. On the genera of Carabidae, with special reference to the fauna of Boreal America. Trans. Amer. ent. Soc. 9: 91-196, pls. 1-10.

_____ 1882. Synopsis of the tribe Lebiini. Trans. Amer. ent. Soc. 10: 126-183

Jeannel, R. 1942. Coleoteres Carabiques, 2me partie. Faune de France 40: 573-1173, figs. 214-368. Paris.

_____ 1949. Coléoptères carabiques de la Region malgache (troisieme partie). Faune de l'Empire français, vol. XI, 767-1146, figs. 365-548.

Jedlicka, A. 1963. Monographie der Truncatipennen aus Ostasien. Lebiinae - Odacanthinae - Brachyninae (Coleoptera, Carabidae). Ent. Abh. Ber. Mus. Tierk. Dresden, 28: 269-579.

King, P. B. 1958. Evolution of modern surface features of Western North America, p. 3-60. In C. L. Hubbs, (ed), Zoogeography. Amer. Assoc. Adv. Sci. Symp., Washington, D.C.

LeConte, J. L. 1848. A descriptive catalogue of the geodephagous Coleoptera inhabiting the United States east of the Rocky Mountains. Ann. Lyc. Nat. Hist. New York 4: 173-474.

_____ 1851. Descriptions of new species of Coleoptera from California. Ann. Lyc. Nat. Hist. New York 5: 125-184.

Leng, C. W. 1920. Catalogue of the Coleoptera of America, north of Mexico. Mount Vernon, N. Y., 470 p.

Lewin, V. 1963. The herpetofauna of southeastern Alberta. Canad. Fld. Nat. 77(4): 203-214.

Lindroth, C. H. 1954. Die larve von Lebia chlorocephala Hoffm. (Col. Carabidae). Opusc. ent. 20: 10-34.

MacGinitie, H. D. 1958. Climate since the late Cretaceous, p. 61-79. In C. L. Hubbs, (ed.), Zoogeography. Amer. Assoc. Adv. Sci. Symp., Washington, D. C.

Madge, R. B. 1967. A revision of the genus Lebia Latreille in America north of Mexico (Coleoptera, Carabidae). Quaest. ent. 3(3): 139-242.

Mannerheim, C. G. Von. 1837. Mémoire sur quelques genres et espèces de carabiques. Bull. Soc. Imp. Nat. Moscou, Vol. 10(2): 3-49.

Martin, P. S. 1958. Pleistocene ecology and biogeography of North America, p. 375-420. In C. L. Hubbs, (ed.), Zoogeography. Amer. Assoc. Adv. Sci. Symp., Washington, D. C.

Mayr, E. 1963. Animal species and evolution. The Belknap Press of Harvard University Press, Cambridge, Mass. 797 p.

Mayr, E., E. G. Linsley, and R. L. Usinger. 1953. Methods and principles of systematic zoology. McGraw-Hill Book Co., Inc., New York. 336 p.

Menetries, M. 1843. Sur un envoi d'insectes de la côte N. O. d'Amerique. Bull. Acad. Imp. Sci. St.-Petersbourg Phys.-Math., 2: 49-64.

Motschoulsky, V. Von. 1850. Dir Käfer Russlands, 9 p. Moscou.

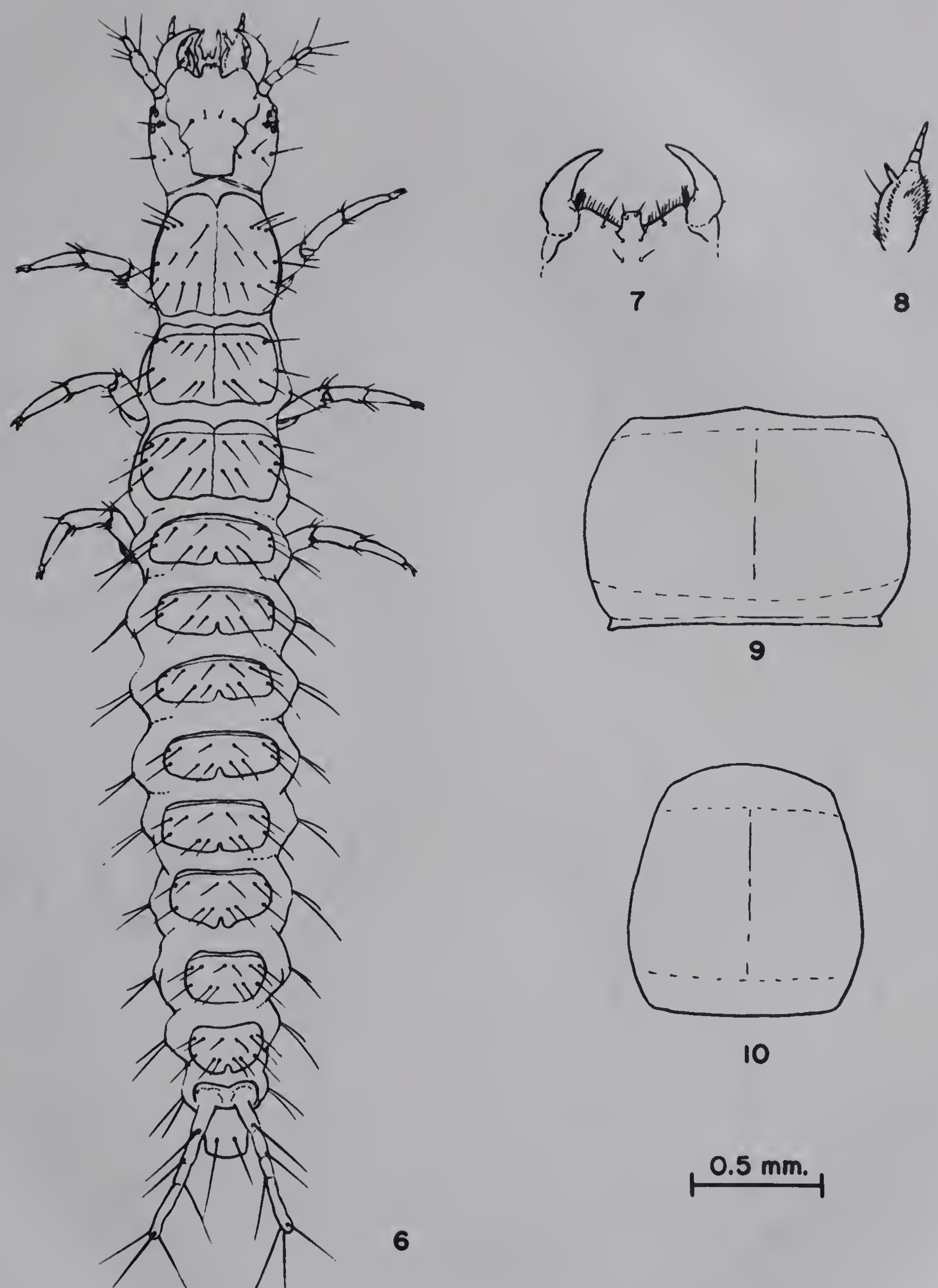
_____ 1859. Coléoptères nouveaux de la Californie. Bull. Soc. Imp. Nat. Moscou 32(2): 122-185.

Say, T. 1823. Descriptions of coleopterous insects collected in the late expedition to the Rocky Mountains, performed by order of Mr. Calhoun, Secretary of War, under the command of Major Long. J. Acad. nat. Sci. Philad. 3(1): 139-216.

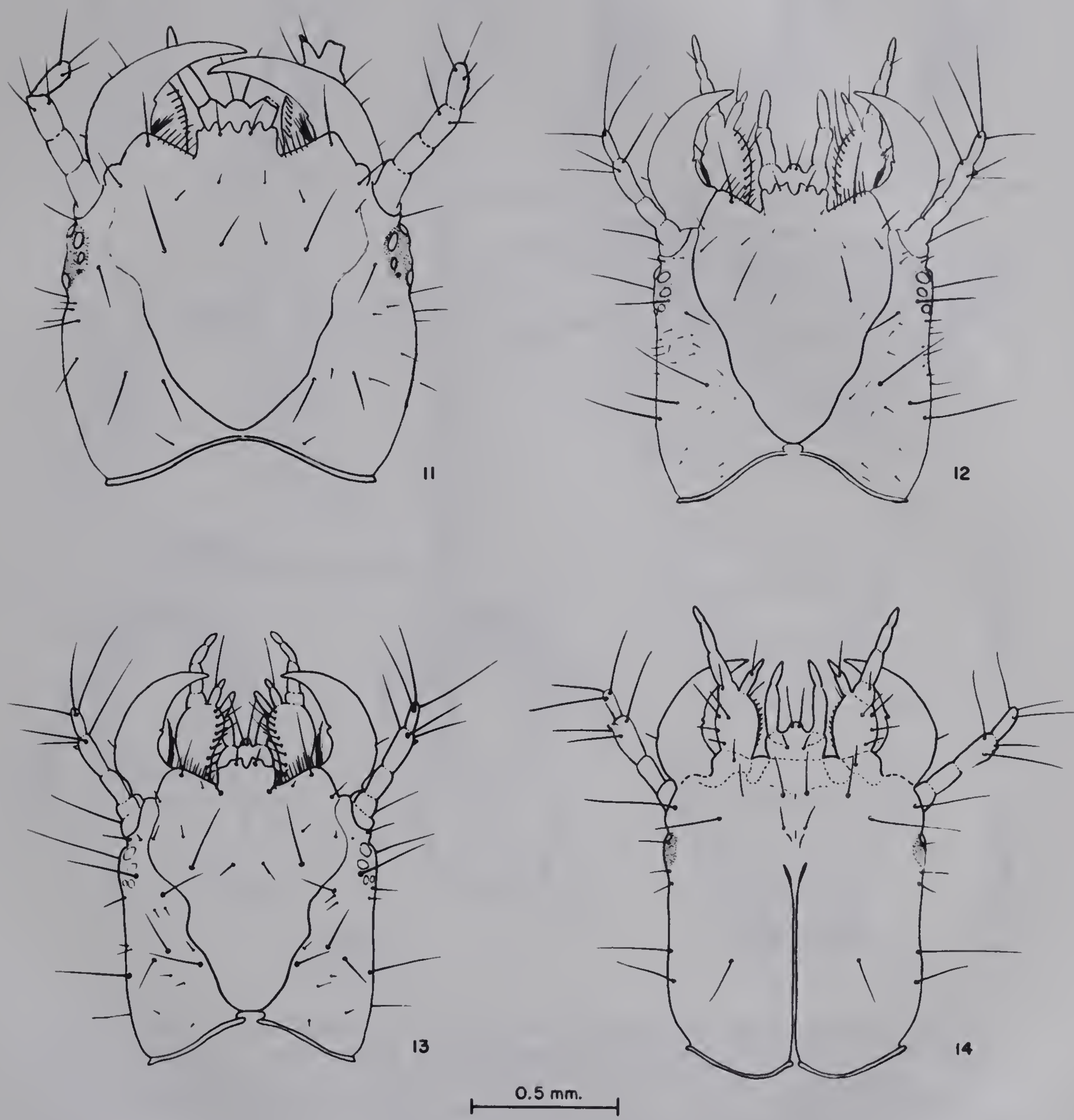
Selander, R. B., and P. Vaurie. 1962. A gazatteer to accompany the "Insecta" volumes of the "Biologia Centrali-Americana". Amer. Mus. Novit. No. 2099, 70 p.

Stanley, J. The discriminant function. A mathematical method for the taxonomic separation of species. MS.

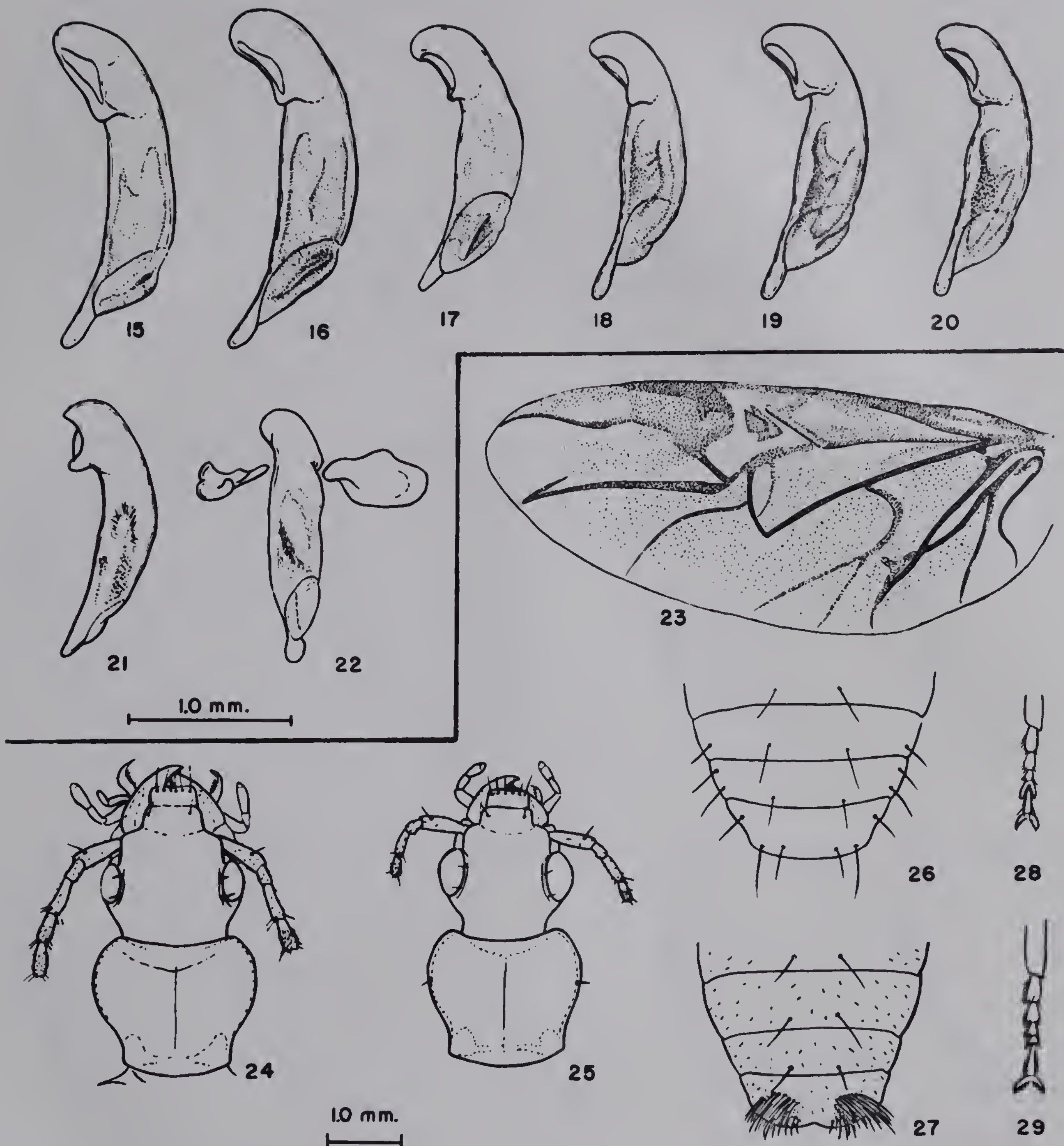
Torre-Bueno, J. R. de la. 1962. A glossary of entomology. Brooklyn Entomological Society, Brooklyn, N. Y. 336 p.



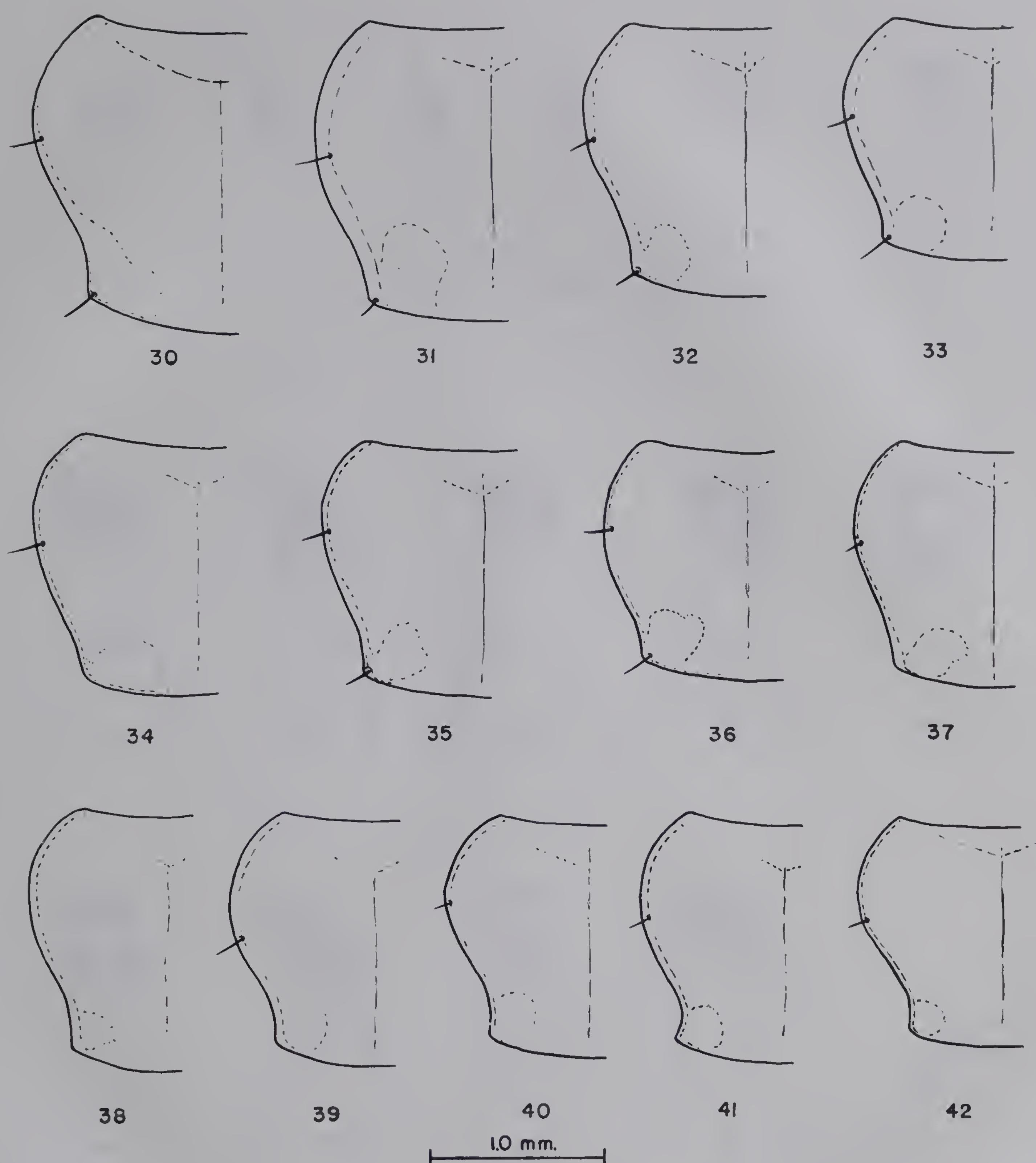
Figs. 6-10. -6. Larva of Tecnophilus croceicollis croceicollis Menetries, first instar (Newark, California). -7. Nasale and mandibles of Plochionus timidus Haldeman. -8. Maxilla of Plochionus timidus Haldeman. -9. Pronotum of larva of Philophuga viridicollis LeConte, third instar, dorsal aspect. -10. Same of Tecnophilus croceicollis Menetries.



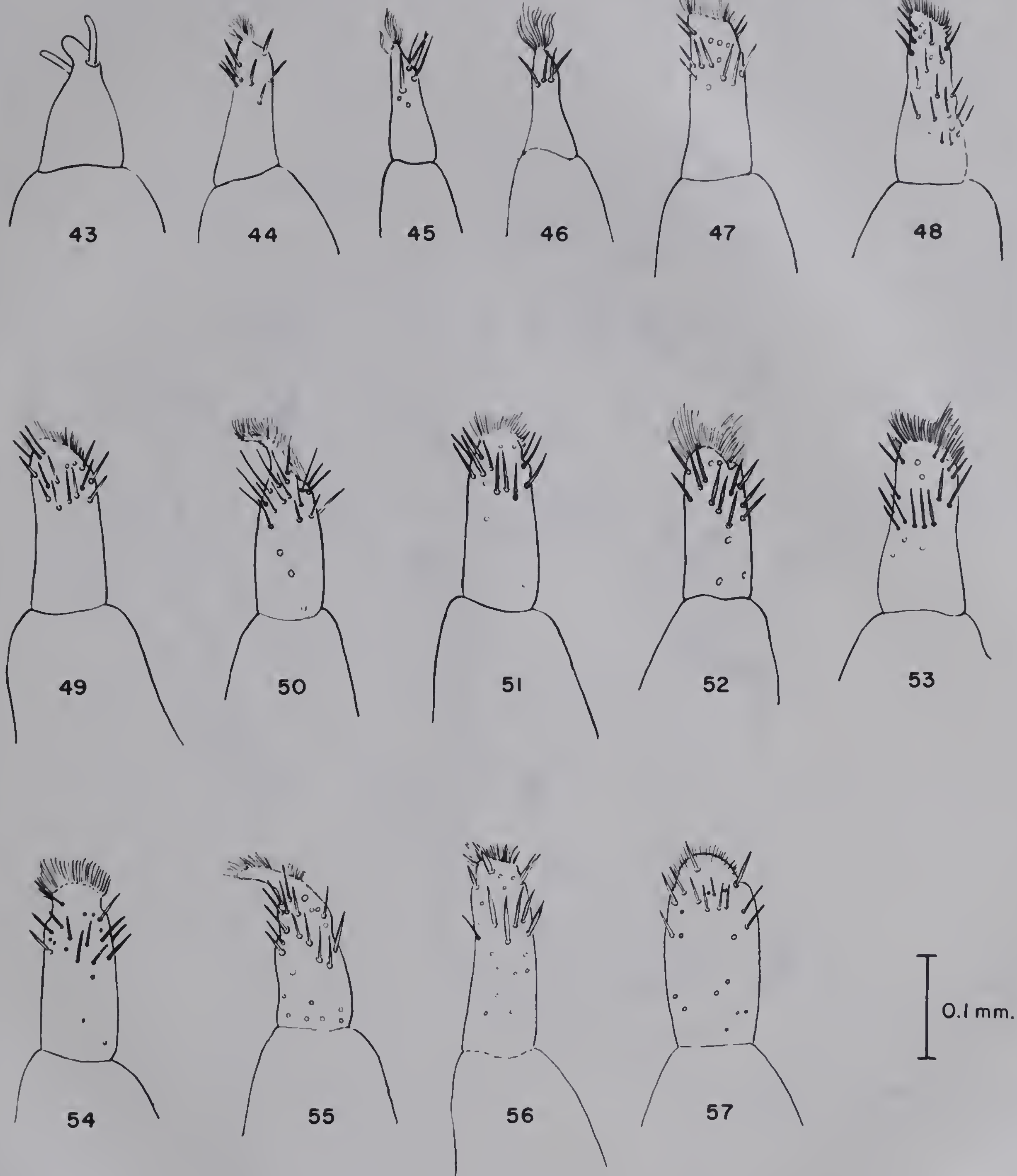
Figs. 11-14. Head capsule, third instar larva. -11. Philophuga viridicollis LeConte. -12. Tecnophilus croceicollis croceicollis Menetries. -13. Tecnophilus croceicollis peigani new subspecies, dorsal aspect. -14. Same, ventral aspect.



Figs. 15-29. -15. Male genitalia of Philophuga viridicollis LeConte, lateral aspect. -16. Same of Philophuga caerulea Casey. -17. Same of Philophuga viridis viridis Dejean. -18. Same of Tecnophilus pilatei Chaudoir. -19. Same of Tecnophilus croceicollis croceicollis Menetries. -20. Same of Tecnophilus croceicollis peigani new subspecies. -21. Same of Infernophilus castaneus Horn. -22. Same of Infernophilus castaneus Horn, dorsal aspect, parameres included. -23. Left wing of Philophuga caerulea Casey. -24. Head and pronotum of Tecnophilus croceicollis peigani new subspecies, dorsal aspect. 25. Same of Tecnophilus croceicollis croceicollis Menetries (Brownsville, Texas). -26. Abdomen of Plochionus timidus Haldeman, ventral aspect. -27. Same of Infernophilus castaneus Horn. -28. Front tarsus of Callida decora Fabricius. -29. Same of Philophuga viridicollis LeConte.



Figs. 30-42. Pronotum, left half, dorsal aspect. -30. Infernophilus castaneus Horn (Coleville, California). -31. Philophuga viridicollis LeConte (Monahans, Texas). -32. Philophuga caerulea Casey (Nogales, Arizona). -33. Philophuga brachinoides Bates (Nochixtlan, Oaxaca). -34. Philophuga viridis amoena LeConte (Medicine Hat, Alberta). -35. Philophuga viridis horni Chaudoir (Stockton, Utah). -36. Philophuga viridis klamathea new subspecies (holotype, Klamath Fall, Oregon). -37. Philophuga viridis viridis Dejean (San Francisco, California). -38. Tecnophilus pilatei Chaudoir (Brownsville, Texas). -39-41. Tecnophilus croceicollis croceicollis Menetries: 39. Brownsville, Texas; 40. Cuddeback Lake, California; 41. Alviso, California. -42. Tecnophilus croceicollis peigani new subspecies (paratype, Lost River Ranch, Alberta).



Figs. 43-57. Right stylus of female ovipositor, dorsal aspect. -43. Euproctinus trivitatus LeConte. -44. Onota floridana Horn. -45. Plochionus amandus Newman. -46. Plochionus timidus Haldeman. -47. Callida punctata LeConte. -48. Callida viridipennes Say. -49. Callida purpurea Say. -50. Callida decora Fabricius. -51. Philophuga viridicollis LeConte. -52. Philophuga viridis viridis Dejean. -53. Philophuga viridus klamathea new subspecies. -54. Philophuga brachinoides Bates. -55. Tecnophilus pilatei Chaudoir. -56. Tecnophilus croceicollis croceicollis Menetries. -57. Infernophilus castaneus Horn.

Fig. 58. Distribution of <u>Philophuga</u> <u>viridicollis</u> LeConte (★), and <u>Philophuga</u> <u>caerulea</u> Casey (●).

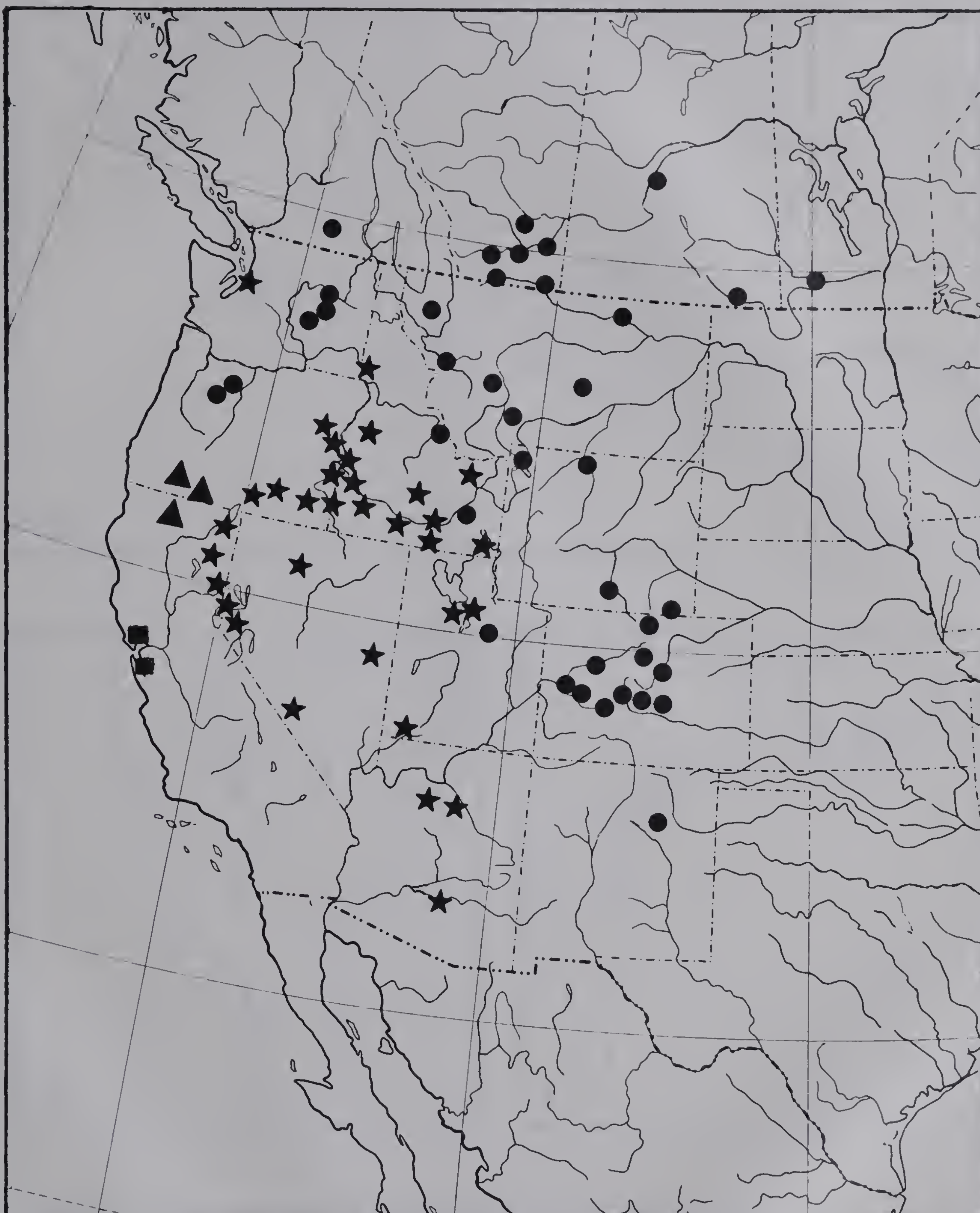
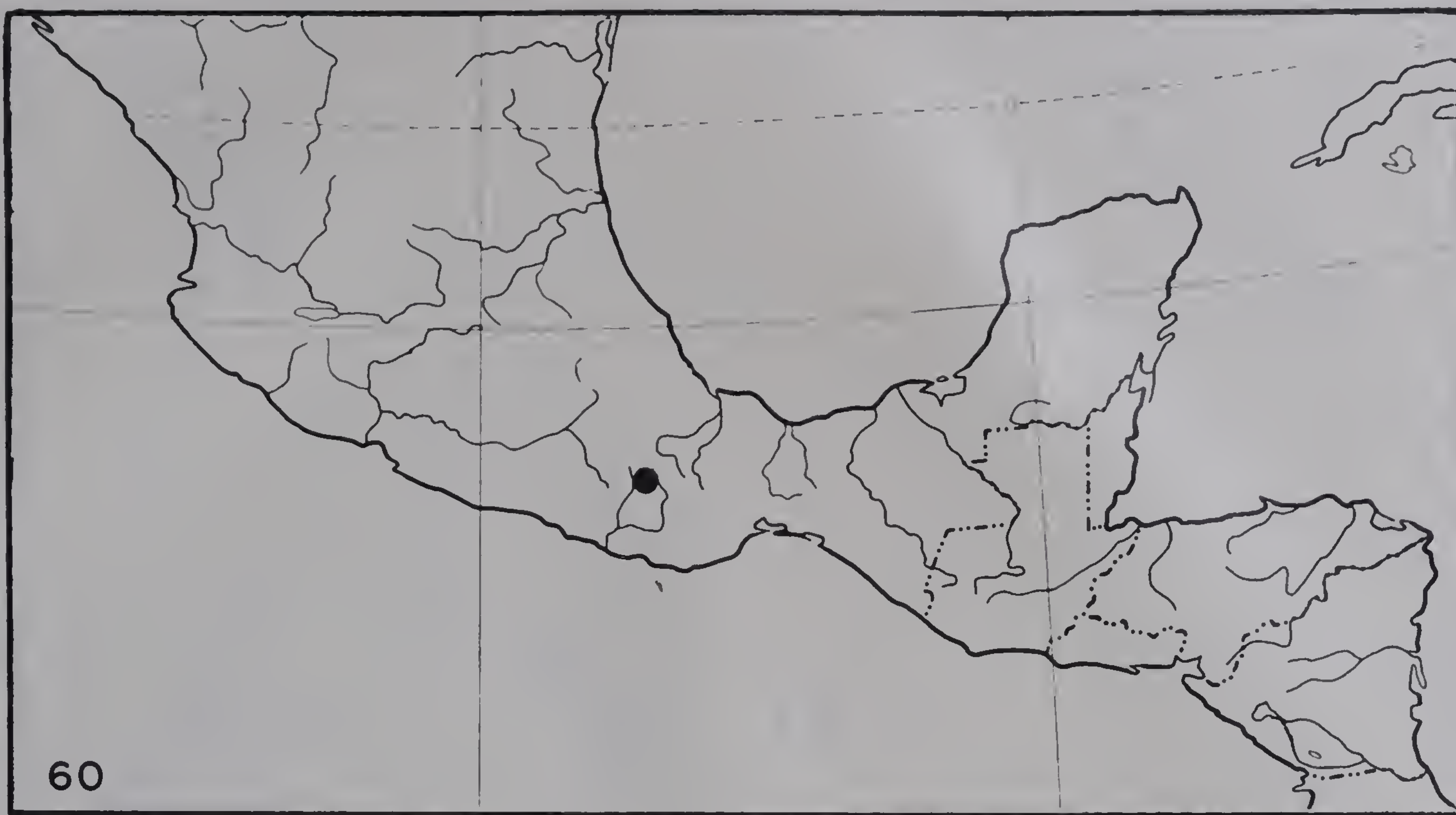
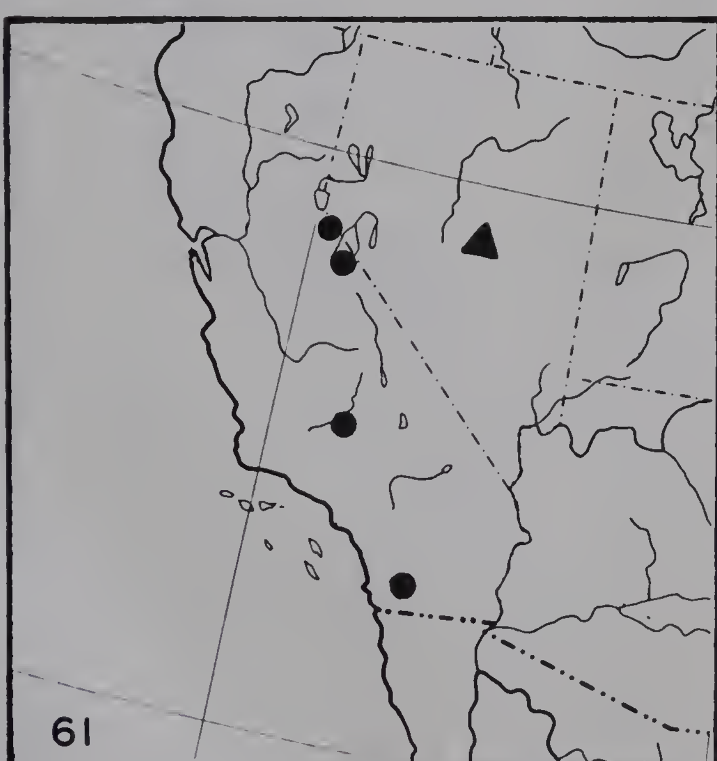


Fig. 59. Distribution of the subspecies of Philophuga viridis Dejean: ■ , v. viridis Dejean; ▲ , v. klamathea new subspecies; ★ , v. horni Chaudoir; and ● , v. amoena LeConte.





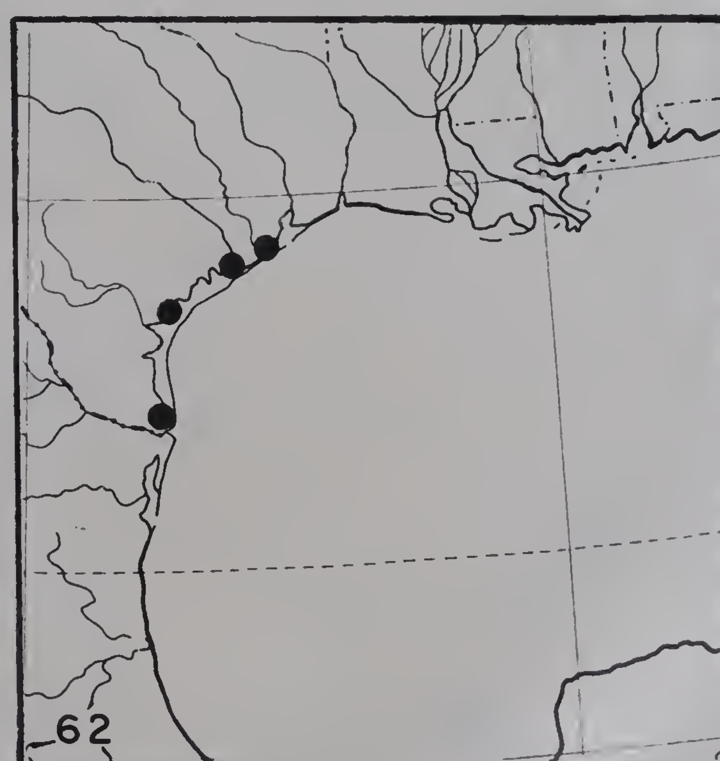


Fig. 60. Distribution of Philophuga brachinoides Bates.

Fig. 61. Distribution of Infernophilus castaneus Horn. ▲ represents a state locality only.

Fig. 62. Distribution of Tecnophilus pilatei Chaudoir.

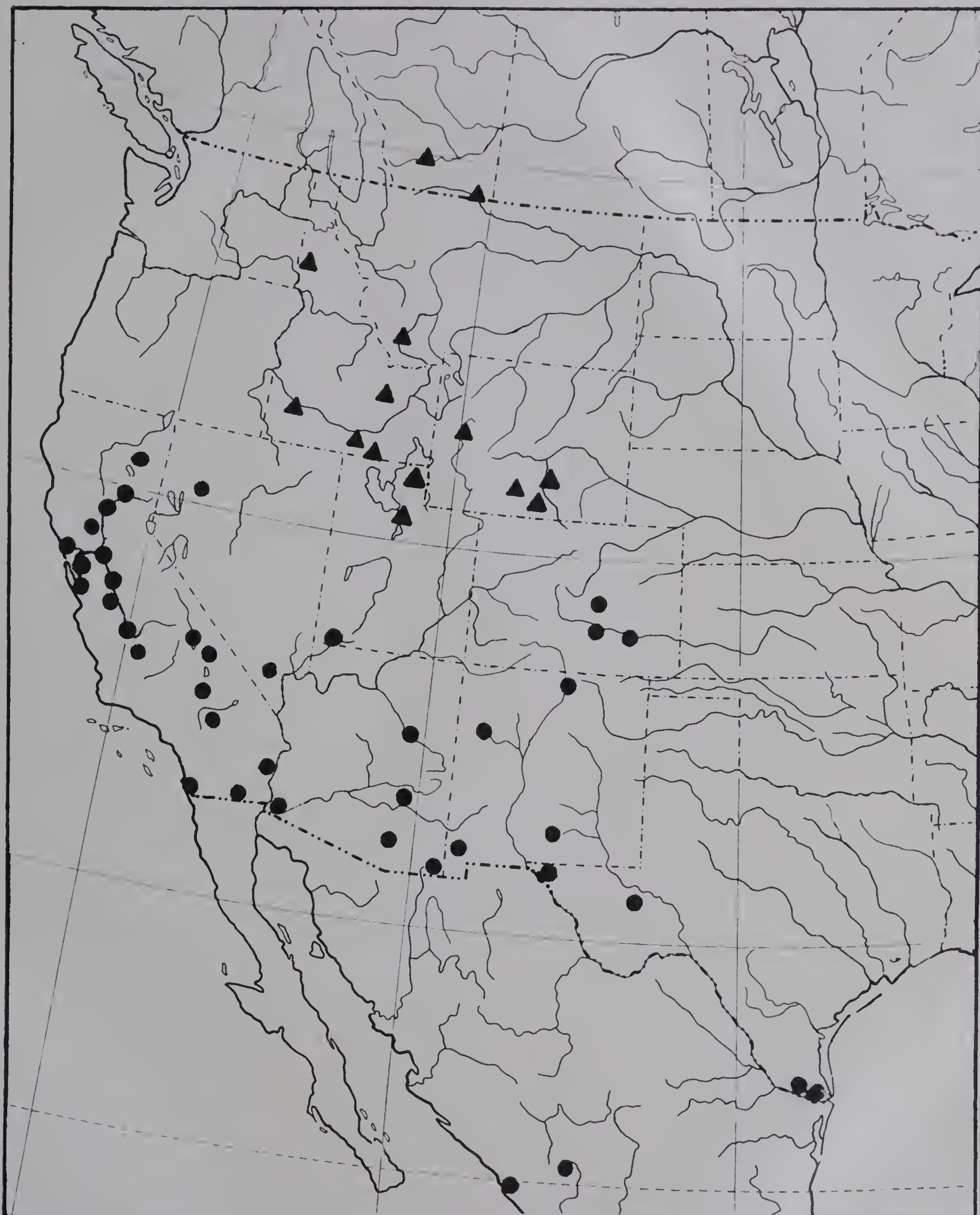


Fig. 63. Distribution of the subspecies of Tecnophilus croceicollis Menetries: ● croceicollis croceicollis Menetries; ▲ croceicollis peigani new subspecies.